Bollettino Malacologico

INTERNATIONAL JOURNAL OF MALACOLOGY

XXXIV 1998

Società Italiana di Malacologia
S.I.M.

Autorizzazione Tribunale di Milano n. 479 del 15 Ottobre 1983
Spedizione in A.P. Art. 2 comma 20/C Legge 662/96 - filiale di Milano
25 Maggio 1998 spedizione n. 1 - 1999

ISSN 5678 8976

QUOTE SOCIALI 1999

CATEGORIE SOCI	ITALIA	ESTERO
Enti, Istituzioni, Sezioni	£ it. 81.000	£ it. 105.000
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Bollettino Malacologico, Roma, **34** (1-4): 1-22, [1998]1999 - Società Italiana di Malacologia

Nervous system development of a primitive pulmonate (Mollusca: Gastropoda) and its bearing on comparative embryology of the gastropod nervous system

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KEY WORDS: Gastropoda - Euthyneura - *Ovatella myosotis* - development - nervous system

ABSTRACT As is typical for primitive pulmonates, the ellobiid *Ovatella myosotis* undergoes a veliger stage during development. The development of the nervous system and sensory organs of this species was examined in detail, using 2 µm serial sections. During the larval phase, three pairs of ganglia in the headfoot (cerebropleural, pedal and buccal ganglia) and three visceral loop ganglia (supraoesophageal, suboesophageal and visceral ganglion) are formed. The first-formed connective from the cerebropleural ganglion to the pedal ganglion is the pleuropedal connective. The pleural ganglia separate from the cerebral ganglia after metamorphosis. Eyes and statocysts are formed by ectodermal invaginations. An osphradial ganglion (the remnant of an osphradium) is formed during the larval phase and reduced at metamorphosis. A detailed discussion on nervous system genesis in gastropods is provided. The development of *O. myosotis* reveals many similarities in the nervous system genesis of pulmonates and opisthobranchs. This allows a critical evaluation of recent studies on other euthyneuran nervous system genesis. The sequence of formation of connectives to the pedal ganglion in *O. myosotis* provides valuable information for an interpretation of these structures in opisthobranch larval nervous systems. This throws light on the question of the position of the pleural ganglion in nudibranchs. Also, it is suggested that the formation of the pleural ganglion from a common anlage (= rudiment) with the cerebral ganglion is typical for higher gastropods.

RIASSUNTO L'ellobiide *Ovatella myosotis* possiede uno stadio di veliger durante il suo sviluppo, come è tipico per i pulmonati primitivi. Lo sviluppo del sistema nervoso e degli organi di senso è stato esaminato in dettaglio attraverso sezioni seriali di 2 µm. Durante la fase larvale si formano tre paia di gangli (cerebropleurale, pedale e gangli buccali) nel complesso cefalopodiale, e tre gangli viscerali (supraesofageo, subesofageo e viscerale). Il primo connettivo a formarsi dal ganglio cerebropleurale a quello pedale è il connettivo pleuropedale. I gangli pleurali si separano dai gangli cerebrali dopo la metamorfosi. Gli occhi e le statocisti si formano per invaginazione ectodermica. Un ganglio osfradiale (il residuo di un osfradio) si forma durante la fase larvale e si riduce alla metamorfosi. Si discute dettagliatamente sulla genesi del sistema nervoso nei gasteropodi. Lo sviluppo di *O. myosotis* rivela molte similarità nella genesi del sistema nervoso con pulmonati ed opistobranchi. Questo permette una valutazione critica di studi recenti sulla genesi del sistema nervoso di altri eutineuri. La sequenza di formazione dei connettivi al ganglio pedale in *O. myosotis* fornisce importanti informazioni per una interpretazione di queste strutture nel sistema nervoso larvale degli opistobranchi. Ciò fa luce sulla questione della posizione del ganglio pleurale nei nudibranchi. Inoltre, si suggerisce che la formazione del ganglio pleurale da un *anlage* (= rudimento) comune con il ganglio cerebrale, sia tipica per i gasteropodi superiori.

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INTRODUCTION

Increasing attention has been paid to anatomical characters of the nervous system in more recent analyses of molluscan and gastropod phylogenetic relationships (Haszprunar, 1988; Nordsiek, 1992; Huber, 1993). The selected characters originate from anatomical studies of adult animals as well as from embryological studies. Embryology was called upon to interpret homology relations of adult structures and was the topic of a number of recent publications. This research, which focused mainly on nudibranch opisthobranchs, led to conclusions extending beyond the systematic level of gastropods (Page, 1992a,b) or even molluscs (Page, 1993). In contrast to opisthobranchs, the pulmonates have hardly received any attention during the last few decades in this regard.

The data on pulmonates are unsatisfactory for two reasons: (1) as opisthobranch studies show, modern techniques provide a substantially more detailed data set and demonstrate the limited reliability of embryological studies carried out with the paraffin section technique; (2) all previous studies on the development of pulmonate nervous systems were restricted to species with direct development, i. e., those lacking the typical veliger larval stage. Direct development while common among pulmonates, is nevertheless a derived condition as in all major gastropod taxa indirect development via a veliger larva is the primitive condition. In direct development the shape of developmental stages and the timing of structure formation are usually substantially altered compared with primitive larval development and therefore the usefulness of species with a suppressed larval stage for comparing developmental processes between higher gastropod taxa is limited.

The ellobiid pulmonate *Ovatella myosotis* (Draparnaud, 1801) has, as is typical for primitive pulmonates, a veliger larva. This larval stage is similar to the primitive planktotrophic euthyneuran larva, although in this species the larval phase is spent inside the egg capsule. *O. myosotis* is very easy to culture and therefore convenient for embryological studies. It is particularly appropriate for developmental studies of the nervous system because the major ganglia in the adults are separated. Consequently, it is possible to interpret nervous system elements of developmental stages by tracing their genesis in reverse direction (form late to early stage). This should be carried out with a method that allows the investigation of developmental processes as continuously as possible. Until now most studies on gastropod nervous system development did not do this sufficiently and described the organisation of more or less isolated developmental stages only.

Contradictory interpretations on the larval nervous system of nudibranch opisthobranchs have recently been published (CARROLL & KEMPF, 1994 vs. PAGE, 1992a,b vs. TARDY, 1970, 1974). Adult nudibranchs have an extremely concentrated arrangement of ganglia. It is surprising that representatives of this group were chosen for recent studies because tracing and interpreting larval elements is extremely difficult if the respective elements are not separate in the adult. The development of *O. myosotis* may provide valuable information on the identity of structures of larval pulmonate and even opisthobranch nervous systems. According to Von Baer's rule (see GOULD, 1977, DENIS & COLLENOT, 1995a,b) the earlier the developmental stages of different species are, the more similar they are. This is also applicable to larvae of euthyneurous gastropods. The available studies on pulmonates with veliger development (FRETTER, 1943; LITTLE *et al.*, 1985) have not revealed any character generally different from that of opisthobranchs and as will be shown, the larval nervous system of pulmonates closely resembles that of opisthobranchs.

The present study may also be useful as basis for future investigations with modern techniques like histochemistry or immunocytochemistry in this species. The knowledge of the general nervous system morphology would be very helpful to carry out studies like RAINERI (1995) or KEMPF et al. (1997) did in other molluscs.

The development of the sensory organs is included in this study because these organs often provide significant information about the nervous system.

MATERIAL AND METHODS

Adult specimens of *Ovatella myosotis* were collected near Alberoni on the Lido di Venezia, Italy. They were cultured in porous flower pots (upper diameter: 24 cm) whose bottoms were filled with a 3-cm layer of substratum taken from the collection site and further covered with coarse potsherds. The bowls were placed in saucers filled with seawater in order to regulate substratum moisture and salinity. The salinity in the saucer was kept between 15 and 35 per mille and the pots were covered with plastic foil to maintain high humidity inside. The snails were fed with standard aquarium fish food. This set up provided a self-reproducing population over many years.

The animals deposited egg masses on the underside of the potsherds or in shallow depressions in the substratum. The egg masses were isolated as follows: Shallow holes (depth: 5 mm; width: 4 mm) were drilled into a piece of ceramic tile. Single egg masses were placed inside these holes. This tile was then covered with a second flat ceramic piece. The entire structure was placed inside the culture bowl at the same level where egg masses were originally deposited. This was the only satisfactory method of isolating egg masses because, in particular, early stages showed a high rate of anomalies and mortality if removed from the culture bowls.

For histological investigation samples of 10 - 15 eggs were taken from isolated egg masses on three to five subsequent days. Specimens were freed from the egg capsule with the help of minute insect needles. Developmental stages younger than six days were fixed in 4 % seawater-buffered formalin before removal from the egg capsule to minimise damage. Older stages were freed from the egg capsule in seawater and subsequently fixed in Bouin's fixativ, which showed better histological results. Developmental stages capable of movement and retraction were anaesthetised prior to removal. For this purpose, samples were put for one to two hours, in a seawater-filled dish to which a drop of ethylene-dissolved menthol was added. Hatched juveniles and adults were anaesthetised in equal parts of 7.5% $MgCl_2$ and seawater or with menthol as described above. Hatched animals were starved for at least 24 hours to clear the gut of sand particles which could negatively effect sectioning. These animals were fixed with Bouin's or Susa's fixative fluid.

Dehydration was carried out in a graded series of ethanol. Specimens up to a size of 3.5 mm were transferred into propylene oxide and embedded in araldite (MOLLENHAUER, 1964). They were sectioned on a Reichert Autocut microtome with ralph glass knives (BENNETT *et al.*, 1976), which were broken on a Reichert ralph knife maker. Two micrometer sections were ribboned with a technique modified from HENRY (1977). A layer of contact cement (Pattex compact, Henkel Co., Vienna) was put on the underside of the block. Staining was done with Regaud's iron hematoxylin or Richardson's methylene-blue - azur II. Larger specimens were transferred to methylbenzoate and benzene and embedded in paraplast. These five or seven µm sections were stained in Heidenhain's azan.

The age of the intracapsular developmental stage was determined as follows: Egg masses were divided into samples which were fixed on different - usually three to five subsequent - days. These sample series covered the entire intracapsular development. The absolute age of each sample was determined by equating identical stages of overlapping sample series. This was controlled by comparing stages with known time of egg deposition.

Four to ten serially sectioned specimens of each day of the intracapsular development period and of a number of hatching stages, juveniles and adults were examined. This high number of investigated specimens enabled the genesis of structures to be followed in a nearly continuos way. Nervous system reconstructions were prepared of specimens at day 5 - 6, 8, 10 - 13, 15, 19, of a hatching stage and of an adult animal. Serial sections were reconstructed by measuring distances on sections with an ocular micrometer on a Reichert Biovar microscope. Contours of resin embedded specimens were established by drawing the embedded specimen with a camera lucida or by measuring distances using the edge of the plastic section as reference. For reconstruction of the adult nervous system, distances of nervous elements to pedal sole and foregut were measured. Photographs were taken on a Reichert Diavar microscope.

RESULTS:

(a) **Adult anatomy:**

The following anatomical data and terminology are important in understanding the developmental processes and the reasoning behind the discussion in this study.

The general organisation of the adult nervous system of *Ovatella myosotis* is given in figure 1. In the adult animal the cerebral ganglia are strongly asymmetrically arranged because the penis complex causes the right ganglion to lie more posteriorly and ventrally than the left one (Fig. 1). The procerebrum (Fig. 1, PR) is an anteriorly separated portion of the cerebral ganglion, which is innervated by two nervous junctions, the anterior and posterior procerebral connectives. These connectives are positioned next to the anterior and posterior ends of the procerebrum. The procerebrum is the base of the tentacular nerve (Fig. 1, TN), which splits into three branches in some distance from the procerebrum. Fibers of the optic nerve (Fig. 1, ON), which emerges near the tentacular nerve, can be traced to the small posterior procerebral connective, which is formed by these fibers. The cerebral gland (Fig. 1, CG) is consisting of a remarkable structure, a duct with a tiny lumen leading from the procerebrum to the body surface at the lateral base of the tentacle, where it opens with a pore. The cerebral commissure (Fig. 1, CC), the connectives to the ganglia, and all other nerves emerge from the main portion of the cerebral ganglion. There are three anteroventrally emerging labial nerves on the left side and two on the right side (Fig. 1, L1 - L3). The penis nerve (Fig. 1, PSN) emerging from the right cerebral ganglion corresponds to one labial nerve from the left side (Fig. 1, L1). The statocyst nerve (Fig. 1, SN) emerges posteriorly between the cerebropedal and the cerebropleural connective. Dorsally the cerebral ganglion is covered with a cap of presumably neurosecretory tissue (VAN MOL, 1967), the dorsal body (Fig. 1, D).

The pedal ganglia of *Ovatella myosotis* have three ventrally (Fig. 1, VP1 - VP3) and three laterally (Fig. 1, LP1 - LP3) emerging nerves. In addition to the pedal commissure, the pedal ganglia are connected by the parapedal commissure, which emerges from the posterior portion of the ganglia.

The statocysts lie embedded in the pedal ganglia (Fig. 1) adjacent to the origin of the pleuropedal connective. The connectives are lateroanterior to the statocysts. Near its entry into the statocyst, the statocyst nerve is twisted lateroposteriorly around the pleuropedal connective in posthatching juveniles and adults. In this area both nerves are in intimate contact with each other and near the statocysts, the fibers of the statocyst nerve are hardly distinguishable from those of the pleuropedal connective.

The pleural ganglia (Fig. 1, PL) lie very close to the pedal ganglia (hypoathroid condition) and have no nerves. The suboesophageal ganglion (Fig. 1, SBG) gives rise to one dorsal nerve (Fig. 1, SBN). A short distance from the suboesophageal gan-

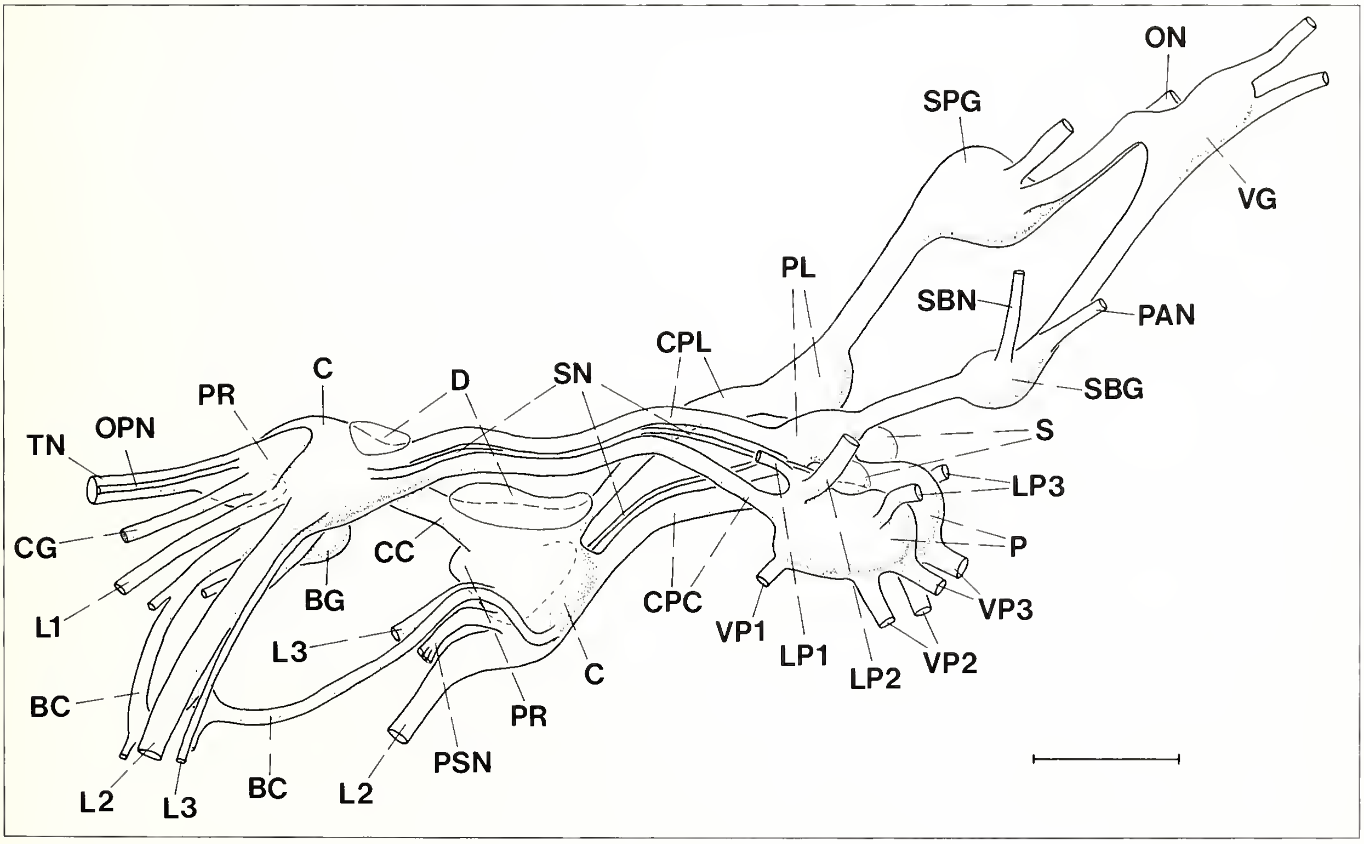


Fig. 1. Reconstruction of the nervous system of an adult specimen of *Ovatella myosotis*. Lateral view from the left side. BC = buccal connective; BG = buccal ganglion; C = cerebral ganglion; CC = cerebral commissure; CG = cerebral gland; CPC = cerebropedal connective; CPL = cerebropleural connective; D = dorsal body; L1-3 = labial nerves; LP 1-3 = lateral pedal nerves; ON = osphradial nerve; OPN = optic nerve; P = pedal ganglion; PL = pleural ganglion; PR = Procerebrum; PSN = penis nerve; S = statocyst; SBG = suboesophageal ganglion; SBN = suboesophageal ganglion nerve; SN = statocyst nerve; SPG = supraoesophageal ganglion; TN = tentacle nerve; VG = visceral ganglion; PAN = pallial nerve; VP 1-3 = ventral pedal nerves. Scale bar = 40 µm

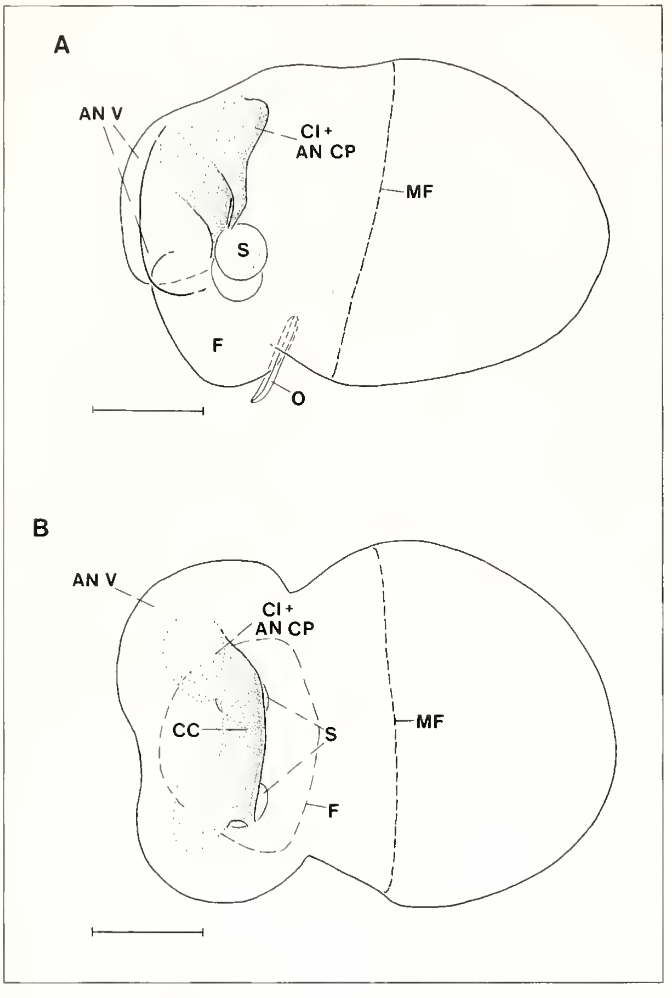


Fig. 2. Reconstruction of the nervous system of a 6-day-old larva of *Ovatella myosotis*.. A. Lateral view from the left side. B. Dorsal view. AN CP + CI = anlage of the cerebropleural ganglia plus cerebral invagination; AN V = anlage of the velum; CC = cerebral commissure; F = foot; MF = mantle fold; O = operculum; S = statocyst. Scale bar = 40 µm.

glion another nerve (Fig. 1, PAN) emerges from the connective connecting suboesophageal and visceral ganglion. The visceral ganglion (Fig. 1, VG) has two large nerves exiting posteriorly. Besides the strong osphradial nerve (Fig. 1, ON), two other nerves (only one visible in Fig. 1) emerge from the supraoesophageal ganglion (Fig. 1, SPG).

(b) Development:

Nervous system:

The paired ganglia of the headfoot and their commissures:

Cerebral and pleural ganglia:

At development day five (day 5 = 5th day after egg deposition), an ectodermal area at the anterior end of the larva, dorsal to the foregut, staines distinctly darker than the surrounding epithelium. It is located directly at the animal pole of the embryo, which is marked by the attached polar bodies. This is the first visible structure of the nervous system and represents the formation zone of the cerebral commissure. It also contributes to the formation of the cerebral and pleural ganglia.

A few hours after the formation of this first anlage, the cerebral commissure can be distinguished at its center. It consists of a row of ectodermal cells, showing dark-staining nervous fibers at their inner base. Subsequently, the ectoderm on both sides of the cerebral commissure thickens. These thickenings lie in the center of each developing velar lobe (Fig. 2). They soon become multicellular by proliferation. Slight invagination troughs are formed in the center of each anlage (Figs. 19, 21), which first appear on development day 7. The structures surrounding the invagination troughs will henceforth be referred to as cerebral invaginations. As predecessors of various sensory and nervous structures in the head area, they play a major role in further development (Fig. 22).

Initially, the cells of the cerebral commissure have a wide

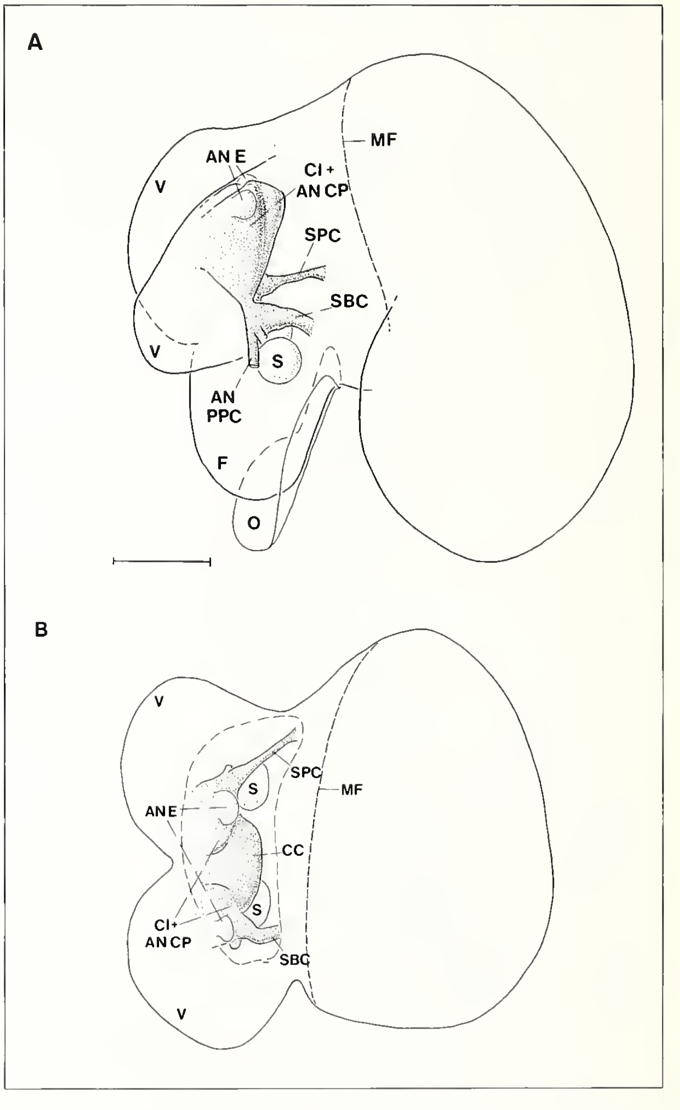


Fig. 3. Reconstruction of the nervous system of an 8-day-old larva. A. Lateral view from the left side. B. Dorsal view. AN CP + CI = anlage of the cerebropleural ganglia plus cerebral invagination; AN E = anlage of the eye; AN PPC = anlage of the pleuropedal connective; CC = cerebral commissure; F = foot; MF = mantle fold; O = operculum; S = statocyst; SBC = suboesophageal connective; SPC = supraoesophageal connective; V = velar lobes. Scale bar = 40 µm.

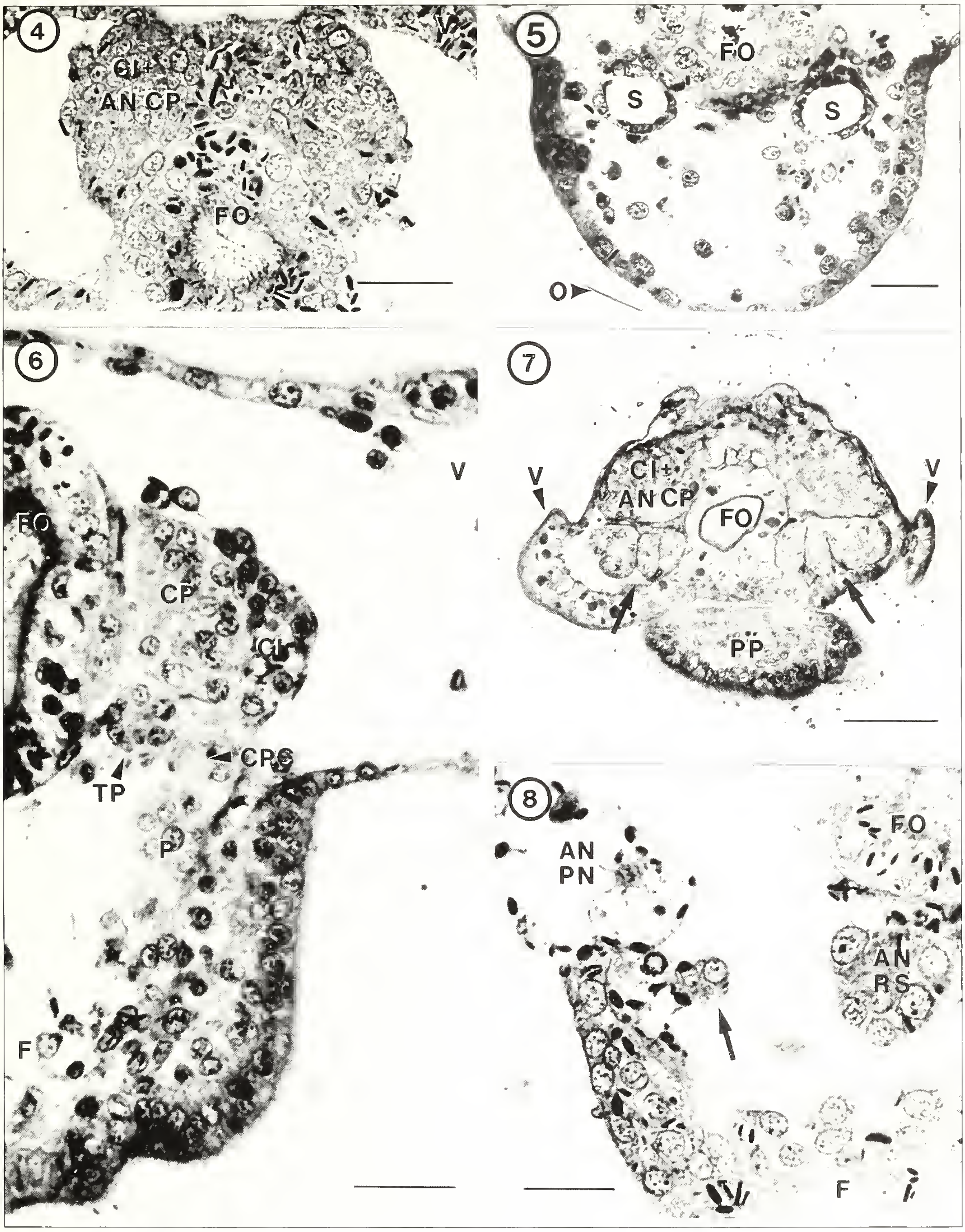


Fig. 4. Cross section through the anterior portion of a 7-day-old larva. AN CP + CI = anlage of the cerebropleural ganglia plus cerebral invagination (only marked on right larval side = left side on figure); FO = foregut; V = velum. Scale bar = 20 µm. Fig. 5. Cross section through the foot of an 8-day-old larva. The lumen contains the cells that form the pedal ganglia. FO = foregut; O = operculum; S = statocysts. Scale bar = 20 µm. Fig. 6. Cross section through the anterior nervous system elements of the left side of a 13-day-old larva. CI = cerebral invagination; CP = cerebropleural ganglion; CPC = cerebropedal connective; F = foot; FO = foregut; P = pedal ganglion; TP = temporary portion of the cerebral ganglion; V = velum. Scale bar = 20 µm. Fig. 7. Cross section through the anterior region of a 12-day-old larva of *Haminoea navicula* showing three pairs of accessory ganglia of the labiotentacular nerve (arrows) (Courtesy of Kurt Schaefer, 1992). AN CP + CI = anlage of the cerebropleural ganglia plus cerebral invagination (only marked on right larval side = left side on figure); FO = foregut; PP = propodium; V = velar lobes. Scale bar = 50 µm. Fig. 8. Cross section through the right side of a 7-day-old larva showing the first anlage of the supraoesophageal ganglion (arrow). AN PN = anlage of the protonephridium; AN RS = anlage of the radula sac; F = foot; FO = foregut. Scale bar = 15 µm.

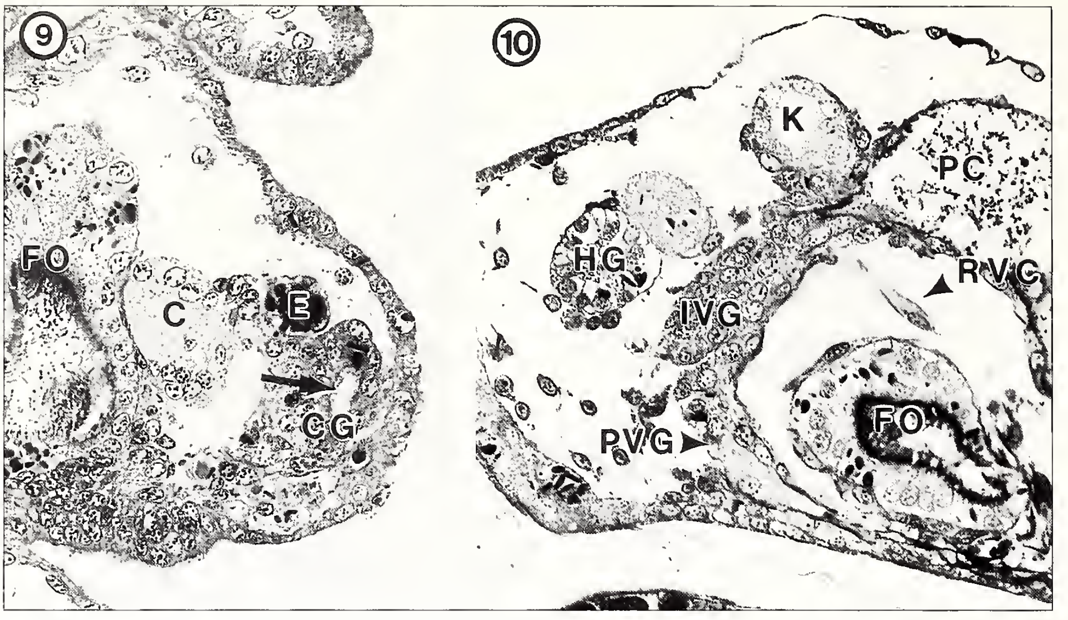


Fig. 9. Cross section through a newly metamorphosed juvenile (15 days) (same specimen as figure 16) in the region of the forming right tentacle. E = eye; FO = foregut; C = cerebral ganglion; CE = cerebral gland; arrow shows the lumen of the forming cerebral gland. Scale bar = 20 µm. Fig. 10. Cross section through a 12-day-old larva showing the region of the forming visceral ganglion. FO = foregut; HG = hindgut; IVG = invaginated portion of the visceral ganglion; K= kidney; PC = pallial cavity; PVG = proliferated portion of the visceral ganglion; RVC = right visceral connective. Scale bar = 20 µm.

cell body and are connected to the ectoderm. The commissure fibers are continuous with fibers which project ventrally. Some of these fibers project towards the statocyst, the others project towards the site of the forming pedal ganglia. As will be shown, the latter nerve branch represents the anlage of the pleuropedal connective (Fig. 3A, AN PPC). A connection with the statocysts is first recognisable by the end of day 5. The inner portion of the cerebral invaginations is in intimate contact with nervous material which is continuous with the cerebral commissure and the ventrally projecting nerve. As will be shown, this nervous material represents the common anlage of the cerebral ganglia (except the procerebrum) and pleural ganglia. This common anlage will henceforth be referred to as the cerebropleural ganglia. The cells for the anlage apparently originate from the posterior portion of the cerebral invaginations, where rapid cell proliferation takes place. This assumed cell migration from the cerebral invagination to the anlage of the cerebropleural ganglia may explain why no boundary is visible between the two structures (Fig. 4).

The cerebral invaginations soon project conspicuously inwards (Fig. 21). Mitotic figures are abundant in sections of these structures. The cerebral invaginations consist of densely packed cells without nervous fibers. The anlagen of the cerebropleural ganglia have fewer cell bodies and consist mainly of nervous fibers (Fig. 14, CP).

On development day 6 the cerebral commissure becomes separated from the epidermis and displaced interiorly. A single, median connection to the epidermis is maintained. This connection is retained throughout the remaining veliger stage. The cerebral commissure contains cell bodies over its entire length throughout the larval period. The nuclei lie on the side of the cells which is closer to the exterior of the animal. No trace of a cephalic sensory organ could be found in the middle of the cerebral commissure and the overlying ectoderm, the site of the usual location of this organ in gastropod larvae.

The cerebropleural ganglia grow until day 9, when they extend ventrally halfway down the oesophagus. They then start to undergo differentiation processes which lead to the formation of the adult elements as well as an additional structure which is only temporary present. The latter, referred to as the temporary portion, separates from the median side of the ganglion anlage on day 11. It is most conspicuous on 13 day, when it is spherical and contains 15-20 nuclei arranged on its outer layer (Fig. 6, TP). It apparently plays a role in the formation of certain nerves (see below). The temporary portion is present until the hatching stage, when it becomes fused with the remaining cerebral ganglion.

Shortly after the differentiation of the temporary portion, the cerebral invagination (= the prospective procerebrum plus cerebral gland) becomes distinctly separated from the rest of the cerebropleural ganglion (Fig. 6, 22C). A membrane forms between the two structures; it may be related to the formation of a cover membrane around the whole ganglion. Although undetectable in earlier developmental stages the separation of the cerebral invagination from the remaining ganglionic anlage may have existed earlier. Both procerebral connectives (first visible on day 13) develop from the junction of the posterior end of the procerebrum-cerebral gland anlage with the remaining ganglion.

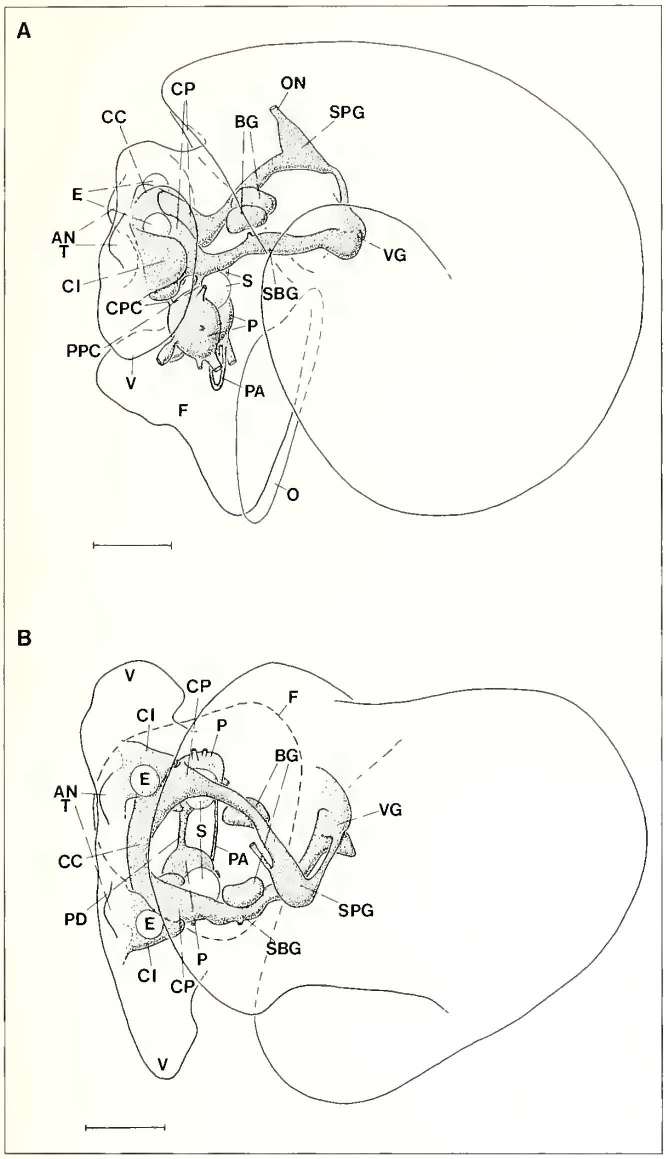


Fig. 11. Reconstruction of the nervous system of a 13-day-old larva. A. Lateral view from the left side. B. Dorsal view. AN T = anlage of the tentacles; BG = buccal ganglion; CC = cerebral commissure; CI = cerebral invagination; CP = cerebropleural ganglion; CPC = cerebropedal connective; E = eye; F = foot; O = operculum; ON = osphradial nerve; P = pedal ganglion; PA = parapedal commissure; PD = pedal commissure; PPC = pleuropedal connective; S = statocyst; SBG = suboesophageal ganglion; SPG = supraoesophageal ganglion; V = velar lobe; VG = visceral ganglion. Scale bar = 50 µm.

At metamorphosis the junction of the procerebrum anlage with the ectoderm and the procerebral invagination troughs narrows considerably; this is caused by the inward movement of the whole ganglionic complex (Fig. 9, 16). This process eventually leads to the condition in which the procerebrum-epidermis connection consists of a narrow tube. Thus, the cerebral tube (the distal portion of the cerebral gland) achieves its typical, elongated, adult shape. At hatching the most distal portion is already tubiform (Fig. 17). This process is illustrated in figure 22.

The pleural ganglia are formed by separation from the larval cerebropleural ganglia. Their initial position corresponds to the site where the pleuropedal connectives emerge from the cerebropleural ganglion. The separation is a slow process beginning on day 11, when the larval cerebropleural ganglion elongates posteriorly. At hatching, separation is completed by a distinct movement of the pleural ganglion in a posterior direction (Fig. 17). At this time the pleural ganglion is still closer to the cerebral than to the pedal ganglion; this represents an epiathroid condition (Fig. 17). The hypoathroid condition, in which the pleural ganglion is closer to the pedal ganglion, is achieved several weeks after hatching. Figure 23 illustrates the formation sequence of the cerebral and pleural ganglia and their connectives to the pedal ganglion.

The first distinguishable elements of the dorsal bodies appear a few weeks after hatching (shell length: 1 mm). These are cells of presumably mesodermal origin attached to the cerebral ganglion near the origin of the cerebral commissure. The dorsal bodies achieve their typical cap-like shape about six weeks (shell length: 2.3 mm) after hatching.

Pedal ganglia:

Immediately prior to the appearance of the pedal ganglia at the end of day 8, sections show a large number of cells in the haemocoel of the foot (Fig. 5). At the same time the laterofrontal epidermis of the foot is thickened and shows cells on its inner base which appear to be detaching from the epidermis. This arrangement of the elements allows the following mode of development for the pedal ganglia to be postulated: Cells detach from the proliferation zones positioned laterofrontally of the foot. These cells individually move to the future position of the pedal ganglion and aggregate there (lateroventral to the statocysts). The pedal ganglia are initially visible as small cell clusters. Subsequently, they temporarily extend to the ectodermal proliferation zones on the side of the foot (day 9-10), at which time there is no visible boundary between ganglia and proliferation zones. On day 11 the ganglia are again detached from the epithelium and become covered with a membrane.

At the end of day 11 the pedal (Fig. 15) and parapedal commissures are formed by the outgrowth of nervous fibers from the inner fibrous portion of the ganglia. The initial outgrowth of the parapedal commissure is posterior to the pedal commissure.

Buccal ganglia:

The formation of the buccal ganglia starts on day 11. They are formed by cells from the dorsal side of the radula sac posterior to its connection with the oesophagus. When first distinguishable, the anlagen are two cell clusters connected anteriorly with the radula sac. The ganglia attain a spherical shape on days 12-13 (figs. 11A,B, 13).

The primordium of the buccal commissure is preformed by cells, although it could not be determined whether these cells originate from the pre-existing buccal ganglia or by proliferation from the radula sac epithelium in between the ganglia. The commissure first appears on day 13 and contains nuclei until metamorphosis (day 15).

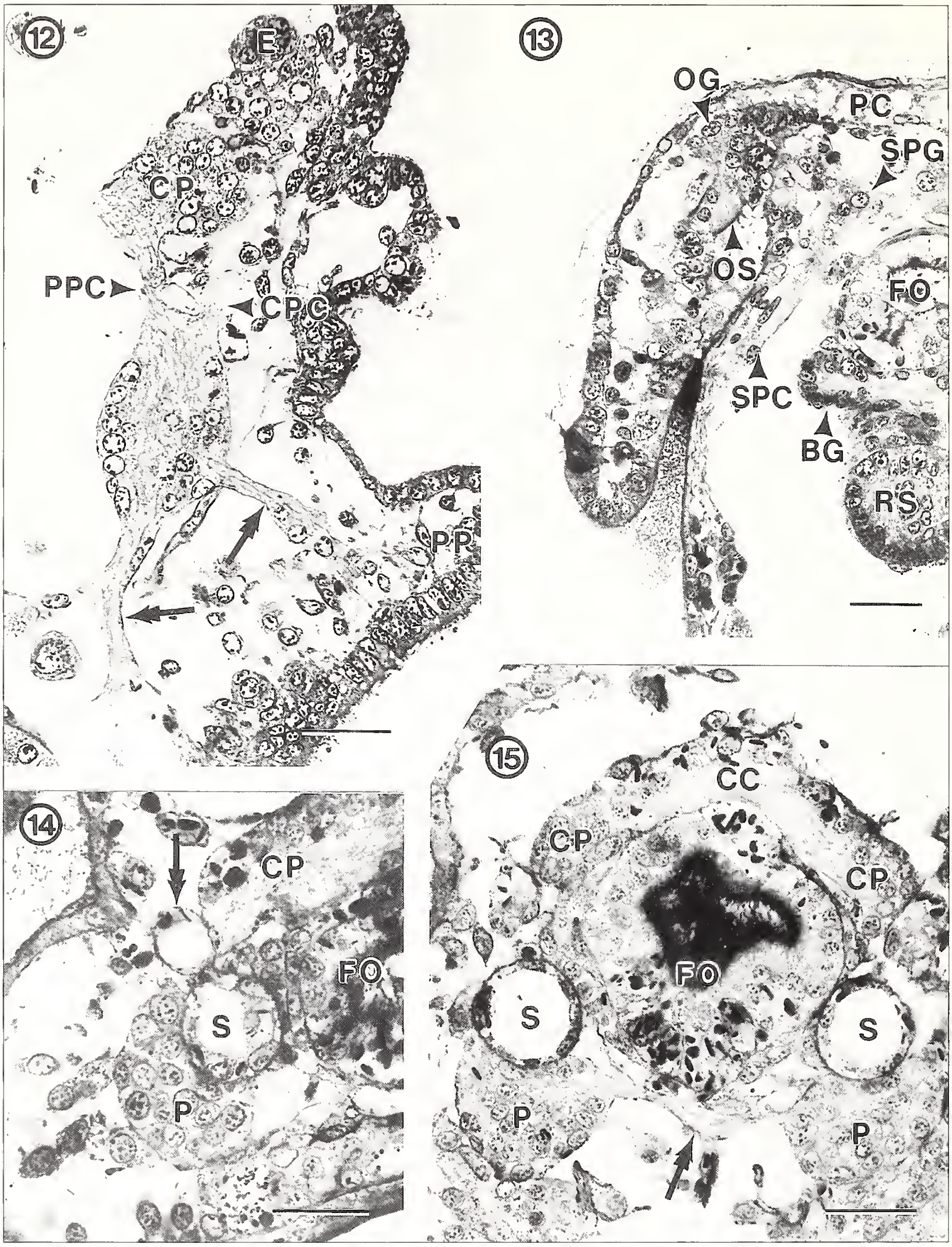


Fig. 12. Parasagittal section through the headfoot of a 13-day-old larva showing two of the pedal nerves (arrows). Note the ganglionic swelling of the anterior pedal nerve in the propodium. CP = cerebropleural ganglion; CPC = cerebropedal connective; E = eye; P = pedal ganglion; PP = propodium; PPC = pleuropedal connective. Scale bar = 20 µm. Fig. 13. Cross section through the right side of a metamorphic competent (day 15) larva. BG = buccal ganglion; OG = osphradial ganglion; OS = osphradium; PC = pallial cavity; RS = radula sac; SPC = supraoesophageal connective, SPG = supraoesophageal ganglion. Scale bar = 20 µm. Fig. 14. Cross section through the right side of a 12-day-old larva showing the static canal of the statocyst (arrow). CP = cerebropleural ganglion; FO = foregut; P = pedal ganglion; S = statocyst. Scale bar = 20 µm. Fig. 15. Cross section through the pedal ganglia of a 12-day-old larva showing the newly formed pedal commissure (arrow). CC = cerebral commissure; CP = cerebropleural ganglion; FO = foregut; P = pedal ganglia; S = statocysts. Scale bar = 20 µm.

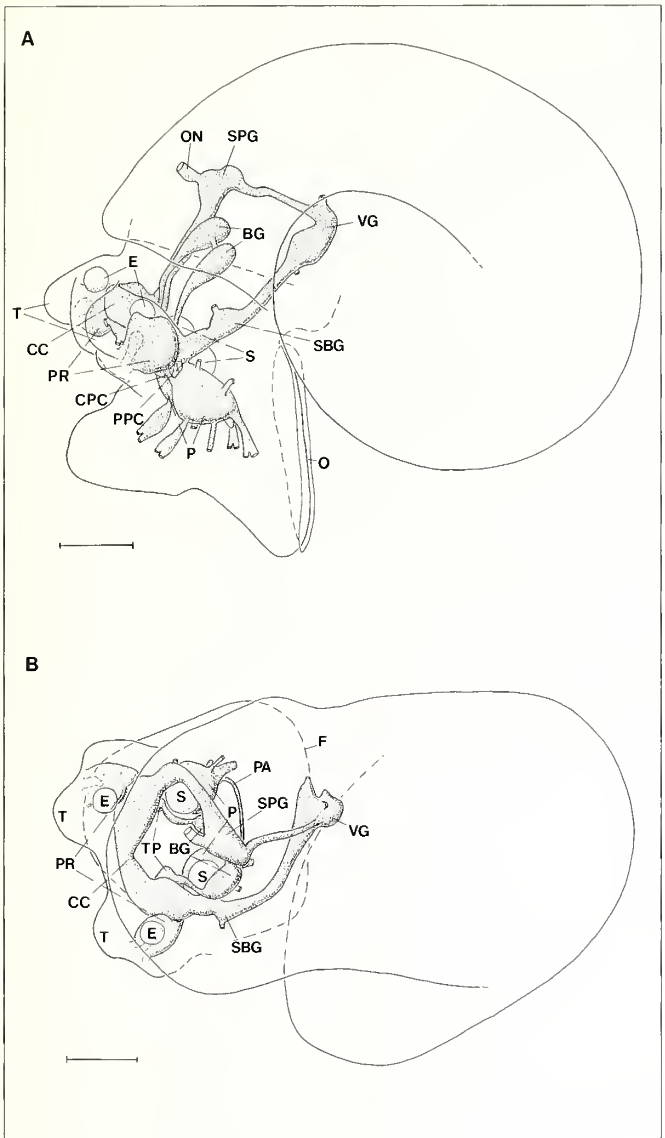


Fig. 16. Reconstruction of the nervous system of a newly metamorphosed juvenile (15 days) A. Lateral view from the left side. B. Dorsal view. BG = buccal ganglion; CC = cerebral commissure; CPC = cerebropedal connective; E = eye; F = foot; O = operculum; ON = osphradial nerve; P = pedal ganglion; PA = parapedal commissure; PPC = pleuropedal connective; PR = procerebrum; S = statocyst; SBG = suboesophageal ganglion; SPG = supraoesophageal ganglion; T = tentacle; TP = temporary portion of the cerebral ganglion; VG = visceral ganglion. Scale bar = 50 µm.

Unpaired ganglia of the visceral portion:

Supraoesophageal ganglion:

The supraoesophageal ganglion is formed through a combination of both invagination and proliferation. The initial primordium appears on day 7 as an aggregation of three to four loosely connected cells directly below the right protonephridium (Fig. 8). These cells presumably originate form an ectodermal proliferation zone slightly dorsal and posterior to the right protonephridium. The primordium is connected with the right cerebropleural ganglion via a connective, which has also formed on day 7. The proliferated portion barely grows until the onset of mantle cavity invagination on day 11. Prior to the mantle cavity invagination, the formation zone of the supraoesophageal ganglion adjoins that of the visceral ganglion. The invagination shifts the supraoesophageal ganglion anlage inside the mantle cavity, where it becomes located in the dorsal epithelium, distinctly to the left of the visceral ganglion. Subsequently, during day 11 the proliferation zone invaginates towards and connects with the already formed portion of the ganglion. Meanwhile the proliferated por-

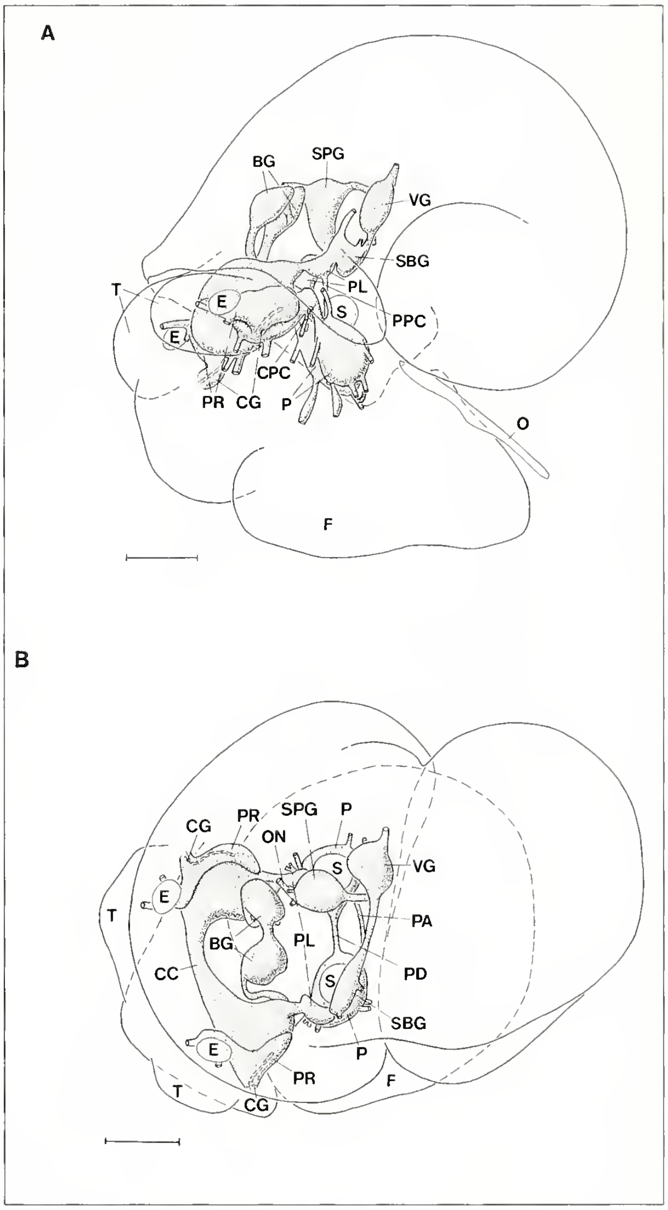


Fig. 17. Reconstruction of the nervous system of a hatching stage juvenile (21 days) A. Lateral view from the left side. B. Dorsal view. BG = buccal ganglion; CC = cerebral commissure; CG = cerebral gland; CPC = cerebropedal connective; E = eye; F = foot; O = operculum; ON = osphradial nerve; P = pedal ganglion; PA = parapedal commissure; PD = pedal commissure; PL = pleural ganglion; PPC = pleuropedal connective; PR = procerebrum; S = statocyst; SBG = suboesophageal ganglion; SPG = supraoesophageal ganglion; T = tentacle; VG = visceral ganglion. Scale bar = 50 µm.

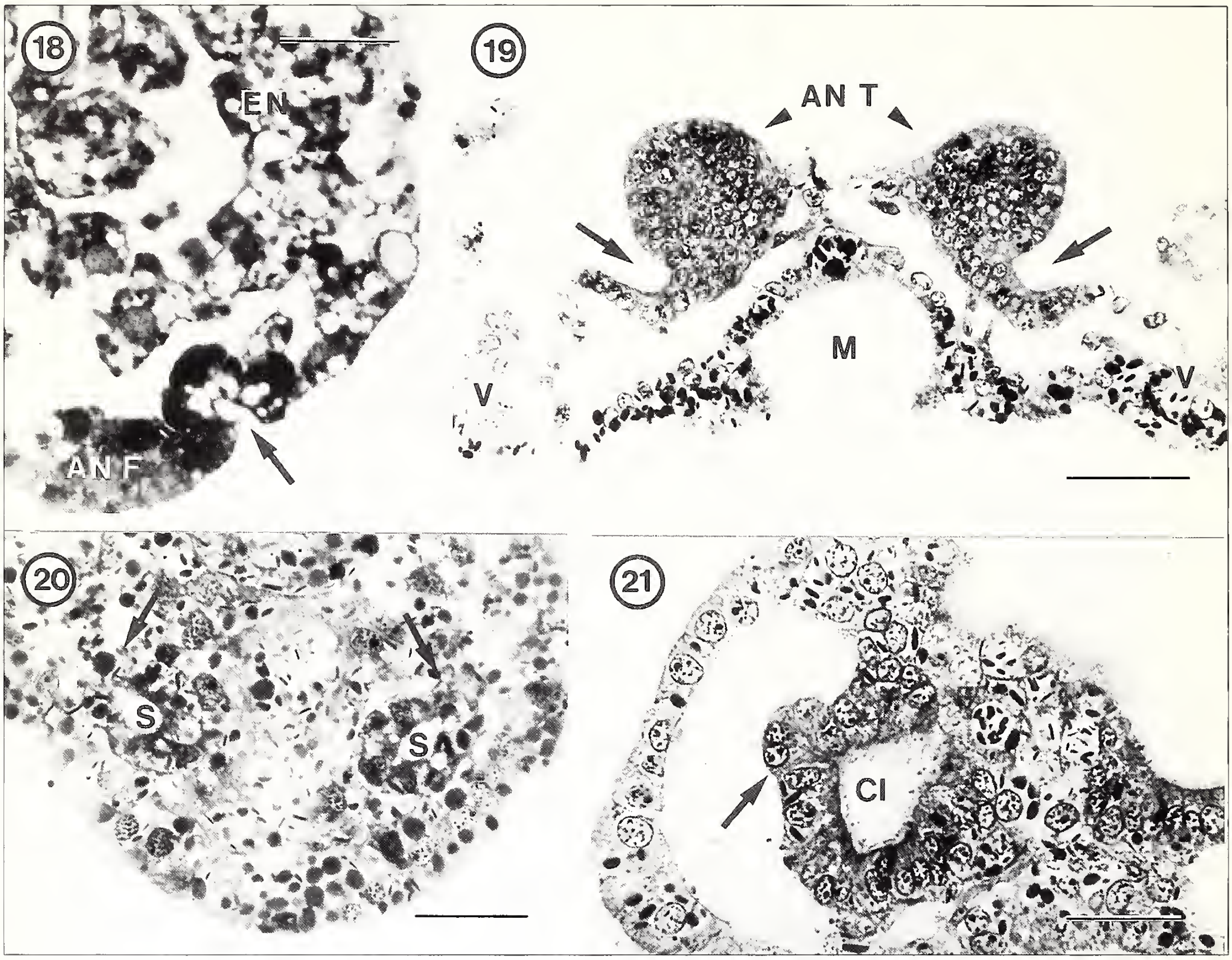


Fig. 18. Cross section through of a 90-hour-old embryo showing the invagination of the left statocyst (arrow). AN F = anlage of the foot; EN = endoderm. Scale bar = 20 µm. Fig. 19. Cross section through the anterior end of a 13-day-old larva showing the relation of the forming tentacles and the opening of the cerebral invaginations (arrows). AN T = anlage of the tentacles; M = mouth opening; V = velar lobes. Scale bar = 30 µm. Fig. 20. Cross section through the foot of a 4-day-old preveliger. Note the dorsolaterally separating portion of the statocysts (arrows). S = statocyst. Scale bar = 20 µm. Fig. 21. Cross section through the right velar lobe and cerebral invagination of an 8-day-old larva showing the invagination of the eye (arrow). CI = cerebral invagination. Scale bar = 20 µm.

tion grows by the attachment of additional cells and becomes compact. Both portions subsequently fuse completely and lose the connection with the ectoderm during day 13.

Visceral ganglion:
The visceral ganglion formation is a combination of the same two processes as in the supraoesophageal ganglion, but in reversed sequence. It starts with an invagination process. The invagination zone is first detectable on day 8 by tracing the fibers of the early-formed left visceral connective. It is positioned in the innermost region of the mantle cavity, which has begun to grow inwards. Thickened epithelial cells form a shallow invagination. Adjacent to this site a mesodermal band projects inwards; it may be confused with elements of the ganglionic anlage. Further invagination of the mantle cavity shifts the anlage of the visceral ganglion posteriorly to a location in the ventral-most epithelium. Subsequently, cells ingress from the invaginated anlage of the ganglion to form a cluster near their site of origin. A narrow junction forms between that cell cluster and the earlier formed epithelial portion of the visceral ganglion anlage, although the cell cluster remains separate. When it first appears, the connective to the supraoesophageal ganglion (right visceral connective) merges with the epithelial, invaginated portion (Fig. 10). On day 12 nervous fibers bridge the junction between the epithelial portion and the inner cell cluster. Figures 10 (IVG, PVG) and 11 (VG) show the two portions of the forming visceral ganglion. Only a small part of the epithelial portion is involved in the subsequent fusion process. The tissue adjacent to the site where the right visceral connective merges with the mantle cavity epithelium fuses with the inner anlage. On day 14 the entire ganglion detaches from the ectoderm.

Suboesophageal ganglion:
The primotdium of the suboesophageal ganglion is first detectable on day 8. It is represented by two cells located ventrally to the left ptotonephridium at the posterior end of the pleurosuboesophageal connective. The origin of these cells, which subsequently increase in numbet, is unclear. They may stem from the pleural ganglion; no associated ectodetmal formation zone could be detected. When the nervous cord ftom the left pleural to the visceral ganglion is completed (day 10), cells attributable to the suboesophageal ganglion are distributed along most of the junction. The nuclei extend from the left cerebropleutal ganglion almost until the visceral ganglion. Until hatching (day 21) there is no distinct ganglion-like thickening visible on that nervous junction (Fig. 11, 16, SBG). At this time, a shift of neurons forms a fibrous connective to the pleural ganglion. Cutrently, the suboesophageal ganglion becomes spherical and grows conspicuously. The formation of the suboesophageal ganglion clearly differs substantially from that of the supraoesophageal and visceral ganglion. The basic difference is the lack of a detectable, associated formation zone. Though one cannot definitely exclude the existence of such a formation zone, the lack of an invagination process is certain. Another major difference is the late differentiation into the typical ganglionic shape, which only occurs after hatching.

Osphradial ganglion:
Cells which proliferate from the earlier fotmed osphtadial epithelium (see below) start forming the osphradial ganglion on day 12 (Fig. 13, OG). At metamorphosis (day 15) it consists of a distinct cluster of cells in close contact with the osphradium. The diffetentiation of a neuropile is first visible on day 18. The ganglion detaches from the epidermis during juvenile development aftet hatching and petsists near its origin throughout life.

Connectives:
Connectives of the headfoot:
The first connectives to be formed are the pleuropedal connectives. They descend from outgtowths projecting ventrally

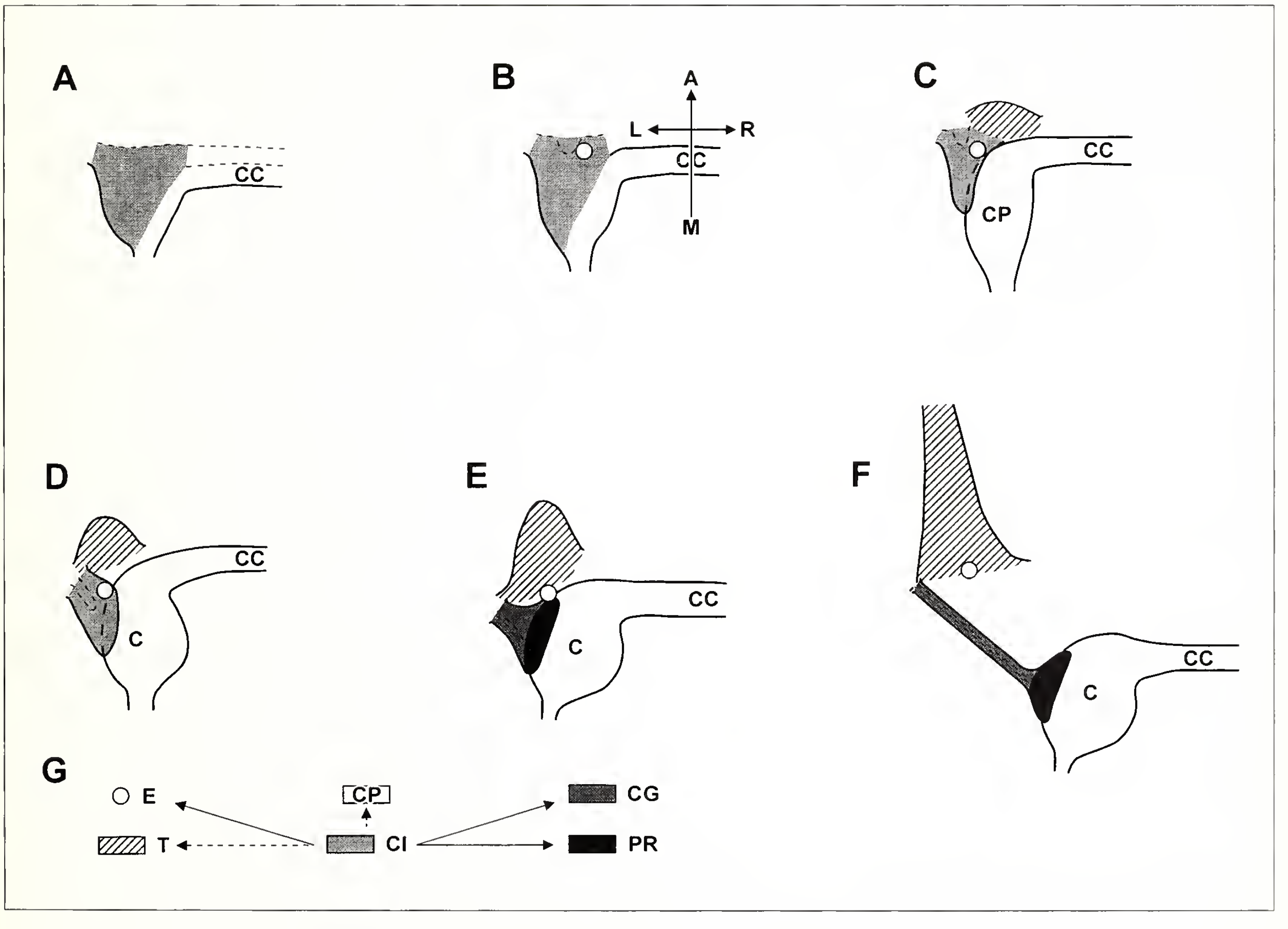


Fig. 22. Diagrammatic sequence of the development of sensory organs and nervous system elements in the head region of *Ovatella myosotis*. A. - F. Dorsal view of the left side; A. Early veliger (day 6) B. Veliger (day 11); C. Late veliger (day 13); D. Postmetamorphic juvenile (day 15) E. Hatching stage; F. Adult; G. Legend for structures derived from the cerebral invagination in A. - F; Stippled arrow if direct derivation is unclear. A = anterior; C = cerebral ganglion; CC = cerebral commissure; CG = cerebral gland; CI = cerebral invagination; CP = cerebropleural ganglion; E = eye; L = left; M = median plane; PR = procerebrum; R = right; T = (anlage of) tentacle.

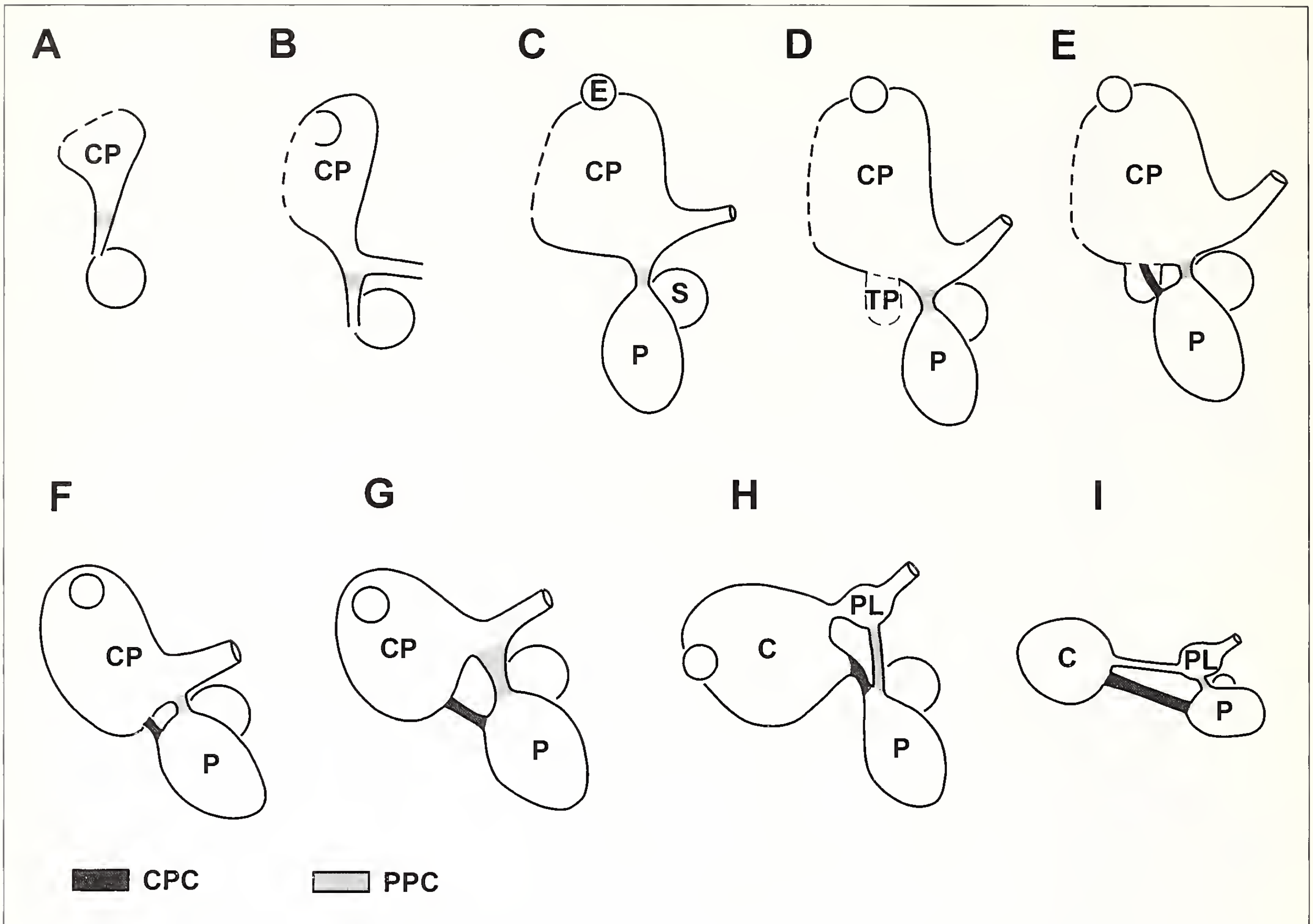


Fig. 23. Diagrammatic sequence of the development of cerebral, pedal and pleural ganglia and the respective connectives of *Ovatella myosotis* (details of cerebral invagination and derived structures not shown). Lateral view from the left side. A. Early veliger (day 6); B. Veliger (day 8); C. Veliger (day 10); D. Veliger (day 11); E. Veliger (day 12); F. Postmetamorphic juvenile (day 15); G. intracapsular juvenile (day 19); H. Hatching stage; I. Adult. C = cerebral ganglion; CP =(anlage of) cerebropleural ganglion; CPC = cerebropedal connective; E = eye (only marked in C.); P = pedal ganglion; PL = pleural ganglion; PPC = pleuropedal connective; S = statocyst (only marked in C.); TP = temporary portion of the cerebral ganglion (only marked in D.). Note that the first-formed connective to the pedal ganglion is the future pleuropedal connective.

from the cerebropleural ganglia. These outgrowths (Fig. 2A) appear shortly after ganglion formation and are initially composed of cells. The two ramifications of the nervous outgrowth extend to the statocysts and to the ectoderm lateral to the statocysts (Fig. 3A). Later (day 10) another ramification, which becomes fibrous in its ventral portion, connects with the forming pedal ganglia. These (paired) ramifications represent the ventral portions of the pleuropedal connectives. During the larval stage, the whole length of the relatively short connectives adjoins the statocysts. They lie anterolateral to the statocysts (Figs. 11A, 16A, 17A). The association of the pleuropedal connective with the statocyst is retained throughout development.

The cerebropedal connectives are first detectable early on day 11 as thin fibrous nerves. They emerge laterally from the cerebral ganglion (Fig. 11A) between the temporary portion and the remaining cerebral ganglion (Fig. 6, CPC). They join the pedal ganglia in a more anterior position than the pleuropedal connectives (Figs. 11A, 12). They may originate as an outgrowth of nervous fibers from the cerebral ganglia towards the pedal ganglia, because in the respective zones, nervous fibers are differentiated later in the pedal than in the cerebral ganglia.

The cerebropleural connectives represent the remainder of the junction between the separating cerebral and pleural ganglia. Shortly before hatching they resemble typical connectives consisting mainly of fibers. The last neurons disappear two days after hatching. Figure 23 provides a semi-schematic outline of the formation mode of the commissures that connect cerebral, pleural and pedal ganglia.

The buccal connectives are first visible prior to metamorphosis. At this time they emerge from the temporary portion of the cerebral ganglion. Figure 16B shows this condition in a postmetamorphic juvenile.

Connectives of the visceral loop:
The supraoesophageal connective connecting the right pleural and supraoesophageal ganglion is formed by a thin outgrowth of cells (day 7). It grows from the pleural portion of the still compact cerebropleural ganglion towards the primordium of the supraoesophageal ganglion (Fig. 3B).

With a slight delay the suboesophageal connective between the left pleural and suboesophageal ganglion is formed in a similar manner. It is first visible on day 8 as a short projection with a terminal thickening, which represents the primordium of the suboesophageal ganglion (Fig. 3B).

When it initially appears on day 10, the right visceral connective is composed solely of fibers and runs adjacent to the epidermis. It passes from the supraoesophageal ganglion to the forming visceral ganglion. Its formation prior to the visceral ganglion indicates a possible origin from outgrowing axons of the supraoesophageal ganglion. Because of the above-mentioned shift of the visceral ganglion it become elongated and is detached from the epithelium during day 11. The nerve then passes to the epidermal site, which is later fused with the proliferated portion of the visceral ganglion (Fig. 11).

The left visceral connective is formed by two elements. The first detectable structures are nervous fibers emerging from the anlage of the visceral ganglion on day 8. They run adjacent to the epidermis and project ventrally. The anterior portion is formed by neurons derived from the suboesophageal ganglion.

The connective later (day 10) becomes fibrous when the neurons aggregate to form the suboesophageal ganglion.

The osphradial connective between the supraoesophageal and osphradial ganglion is initially fairly short (day 12) and of cellular structure. Two days later, after the neurons were dislocated into the osphradial ganglion, it becomes fibrous.

Peripheral nerves (abbreviations refer to the adult in Fig. 1):
The statocyst nerve is not recognisable as a separate nerve until hatching. Like in the adult it is very thin and fibrous and emerges from the cerebral ganglion in the hatching stage. It appears to undergo the following way of development: Beginning on day 5, the statocyst is innervated by branches of the nerve trunk, which also gives rise to the pleuropedal connective (Fig. 3A). The fibers innervating the statocysts presumably split upwards from this trunk before the larval pleural ganglion separates from the cerebropleural ganglion. Ventrally, the statocyst nerve maintains a close contact with the pleuropedal connective (see above).

Most other nerves apparently develop as outgrowing axons from pre-existing ganglia, because they are fibrous when first visible. Their development must be rapid, because halfway extended nerves were never detected.

Two tentacle nerves are present as soon as the cerebral ganglion detaches from the epidermis (after metamorphosis, day 15). They have a common origin from the procerebrum next to the eye. During juvenile development their common base extends so that their bifurcation becomes to lie in some distance to the procerebrum.

Two of the three labial nerves (L1, L2) are present after metamorphosis (Fig. 16A). The third one (L3) appears on day 18. During juvenile development the innervation area of the right labial nerve (L1) becomes the penis complex.

The formation sequence of the ventral pedal nerves proceeds from posterior to anterior. The first-formed (day 11) ventral pedal nerve (VP3) initially emerges at the same point as the parapedal commissure. Soon thereafter, two additional ventral nerves appear (VP1, VP2). The most anterior pedal nerve (VP1) (first visible on day 13) contains a number of neurons, which form a swelling below the pedal ganglion. These neurons are present until hatching and temporarily form an accessory ganglion. This structure and other pedal nerves can be seen in figures 11A, 12, 16A, 17A. The three lateral pedal nerves appear between days 11 and 17. The first one (LP2) extends dorsally. At day 12, a small nerve (LP3) emerges posteriorly. The last nerve (LP1) is the most anterior one (Fig. 17A).

The nerve of the suboesophageal ganglion (SBN) is first detectable after metamorphosis. At hatching another nerve (PAN) becomes visible; it emerges posteriorly from the suboesophageal ganglion (Fig. 17A,B). During post juvenile development the origin of this nerve is shifted posteriorly from the suboesophageal ganglion. The two nerves of the visceral ganglion first appear after metamorphosis (Fig. 16A,B). The osphradial nerve is present shortly after the formation of the supraoesophageal ganglion (day 12). The other supraoesophageal ganglion nerves appear during posthatching juvenile development.

Sensory organs:
Tentacles:
The tentacles arise as exteriorly directed outgrowths of the median lips of the cerebral invaginations (Fig. 19, 22). They are first visible as slight elevations at day 13 (Figs. 11, 19) and become small knobs after metamorphosis (Fig. 16). They elongate to the typical tentacular shape during post-hatching juvenile development.

Statocysts:
The statocysts are formed by ectodermal invaginations (Fig. 18). Starting on day 4, this very rapid process slightly precedes the foot formation. Epidermal contact is lost early on day 5, at which point the anlage is a spherical cluster 16 µm in diameter of five to six cells with a tiny central lumen (diameter: 4 µm). During day 5 the anlage elongates. Subsequently, a small portion partly separates laterodorsally (Fig. 20); this will be termed static canal. At the beginning of day 6 the cells of the anlage start flattening. This process is completed on day 8 and results in the typical cystic shape of the statocyst. Maximum statocyst diameter in the veliger larva is 27 µm. The wall of the static canal attains the same shape (Fig. 14). This structure, which has not yet been reported in ellobiids, persists as a junction between the statocyst and the statocyst nerve in the adult. The ciliation in the statocyst and static canal is first detectable at day 6. The statolith is formed prior to cell flattening. During the veliger stage it grows to about 10 µm. After hatching, the statolith disappears and is replaced by small statoconia (diameter: 2 µm).

Eyes:
Similarly to the statocysts, the eyes are formed by invagination (beginning of day 8). The invagination site is located anterolaterally on the cerebral invagination (Fig. 21). The anlage soon becomes spherical and maintains a lumen, which represents the remainder of the invagination. This lumen enlarges as cells begin to flatten. On day 9, pigment is first deposited on the inner base of the cells. Subsequently, the lens replaces the central lumen. By the end of the veliger phase the lens loses its central position and is located anteriorly inside the eye. The eye formation site becomes incorporated into the procerebrum. One week after hatching the eyes detach from the procerebrum.

Osphradium:
On day 11 a cell with long cilia appears in the epidermis near the opening of the newly formed mantle cavity. It lies close to the giant excretory cell of the right protonephridium and is connected with the anlage of the supraoesophageal ganglion. Subsequently, other densely ciliated cells, are formed. They are columnar, with a basal nucleus. Between day 13 and 16 the outer surface of these cells become slightly protruding. This organ, on the basis of its organisation and innervation, can be identified as the chemoreceptory osphradium (Fig. 13).

The reduction of the osphradium, which is absent in the adults, starts after metamorphosis, simultaneously with the formation of the osphradial ganglion. The cells lose their ciliation and become indistinguishable from the surrounding epithelium. Traces of the osphradial epithelium can be found until development day 18.

DISCUSSION

(a) Adult nervous system of *Ovatella myosotis* and terminology:
Previous descriptions of the gross anatomy of the *Ovatella myosotis* nervous system have been provided by PELSENEER (1894), MEYER (1955) and MARTINS (1996) and differ only slightly from the present investigation. The clear hypoathroid position of the pleural ganglia is recognisable in the figure of Martins only. The reported descending nerves are incomplete and misleading in a some points, as for example Meyer apparently mistook a pedal nerve (herein: LP1) as branch of the statocyst nerve. The terminology used in this paper differs from that of MEYER (1955) and MARTINS (1996) with regard to the parietal ganglion, which is termed the suboesophageal ganglion. MARTINS (1996, Fig. 83) figures a ganglionic swelling with a descending nerve between the "parietal" ganglion and the visceral ganglion which could not be detected in the material investigated in this paper. This structure may be homologous with the base of the pallial nerve (Fig. 1, PAN) lying in the posterior portion of the suboesophageal ganglion. The extreme morphological variability of *O. myosotis* (MARTINS, 1996) may provide an explanation for this difference.

A detailed description of the cerebral ganglion and its nerves was provided by VAN MOL (1967), whose nomenclature is used in this study. He, however, gives incorrect positions for the procerebral connectives (VAN MOL, 1967, Fig. 14), which are described in the median plane of the procerebrum. Also, unlike Van Mol's description, the cerebral commissure emerges medially.

In this study the visceral loop is regarded as the posterior nervous junction between both pleural ganglia and contains the sub-, supraoesophageal and visceral ganglion. This is thought to represent the primitive condition in pulmonates (see discussion). Finally, in contrast with some authors (e.g. BULLOCK, 1965), the pleural ganglia themselves are not regarded as part of the visceral loop.

(b) Justification of the histological techniques for developmental stages:
Light microscopy has two clear advantages over transmission electron microscopy, for the study of organ system development: (a) The investigation of individual specimens requires substantial less effort, allowing a relatively large number of specimens and developmental stages to be examined closely, and the genesis of structures to be followed nearly continuously. (b) Measured three dimensional reconstructions can be prepared therefore enables to follow the development nearly continuously. (c) It is much easier to understand the three dimensional arrangement of components and to prepare detailed measured reconstructions of whole larval nervous systems. Until now, these reconstructions have been lacking in TEM studies of gastropod larvae.

(c) General comparative aspects of gastropod nervous system development:
Cerebral and pleural ganglia:
The first anlagen of the gastropod cerebral or cerebropleural ganglia are thickened ectodermal areas, the cerebral invaginations (also termed cephalic, cerebral or sense plates or "Scheitelplatten"). These paired structures are located in the intravelar area (e. g. *Buccinum*: GIESE, 1978; *Aeolidiella*: TARDY, 1970, 1974; *Melibe*: PAGE, 1992a; *Ovatella*: herein) or in the corresponding position, if no velum is present (e. g. *Pomatias*: CREEK, 1951; *Lymnaea*: REGONDAUD, 1964). This point has found wide agreement among students of gastropod organogenesis. Accounts on subsequent development, however, differ widely. The ganglia are described as being formed by cell proliferation from the cephalic plates or (partly) invagination of the cephalic plates or by a combination of both processes (for a review of the older literature see RAVEN, 1966). The formation of an invagination in the cerebral plates (= cerebral invagination) as in *Ovatella* is common in all gastropod taxa (RAVEN, 1966). Reports vary in regard to what extent the cerebral invaginations contribute to ganglion formation and in the timing of their appearance. The invaginations are regarded as independent structures or as source of material for the ganglia. The latter interpretation is favored in most recent studies (e.g. PAGE, 1992a for *Melibe*; this study for *Ovatella*).

Cerebral ganglion formation in other pulmonates has also

been reported to be very similar to *Ovatella* (*Limax*: HENCHMAN, 1890; *Lymnaea*: REGONDAUD, 1964; RAVEN, 1975). In particular, the formation of the procerebrum and cerebral gland of *Lymnaea* is very similar to that of *Ovatella*.

The temporary median portion of the ganglia in *Ovatella myosotis* (Figs. 6, 16B, TP) resembles the structure Henchman (1890) described for *Limax maximus*. In opisthobranchs, probable homologues were found in *Haminoea navicula* (SCHAEFER, 1992) and *Melibe leonina* (PAGE, 1992a,b). Perhaps one of the two pairs of ganglia in the propodium of dorid nudibranchs is homologous as well, as proposed by PAGE (1993).

Cerebral commissure:

Two completely different ways of cerebral commissure formation have been described in gastropods:

(1) SMITH (1935) for *Patella*, MORITZ (1939) for *Crepidula*, D'ASARO (1966, 1969) for *Thais*, *Bursa* and *Distorsio*, BROWN (1934) for *Philine*, RIEDL (1960) for *Rhodope*, TARDY (1970, 1974) for *Aeolidiella* and SCHAEFER (1992) for *Haminoea* describe it as being preformed by the epithelium between the forming ganglia. This corresponds to my observations in *O. myosotis*.

(2) CONKLIN (1897) for *Crepidula*, DELSMAN (1914) for *Littorina*, CROFTS (1937) for *Haliotis*, ERLANGER (1891a,b, 1892) for *Viviparus* and *Bithynia*, STÖCKMANN-BOSBACH (1989) for *Nucella*, DEMIAN & YOUSIF (1975) for *Marisa*, THOMPSON (1958, 1962) for *Adalaria* and *Tritonia*, SMITH (1967) for *Retusa* and HENCHMAN (1890) for *Limax* describe it as an outgrowth of the pre-existing ganglia.

However, the case of the genus *Crepidula* indicates that some of these observations are erroneous as CONKLIN (1897) or MORITZ (1939) provide completely different descriptions for the same genus. Although CONKLIN (1897) mainly worked on *C. fornica*, he also investigated *C. adunca*, the same species MORITZ (1939) studied. An origin of the cerebral commissure from the epithelium between the ganglia may be generally true in gastropods. This is additionally supported by the presence of the cephalic sensory organ, which may represent a basic feature of gastropod veliger larvae (see below). This organ is innervated by the middle of the cerebral commissure and evidence exists that it is formed prior to the cerebral ganglia (apical organ: SMITH, 1935).

Pleural ganglia:

The opinions on pleural ganglia development of gastropods differ substantially in the literature. These interpretations may be grouped into three categories:

(1) Many authors (e.g. DELSMAN (1914) for *Littorina*, ANDERSEN (1925) for *Viviparus,* CASTEEL (1904) for *Fiona*, RIEDL (1960) for *Rhodope,* SMITH (1967) for *Retusa*, TARDY (1970, 1974) for *Aeolidiella*, KRIEGSTEIN (1977) and JACOB (1984) for *Aplysia*, SCHAEFER (1992) for *Haminoea* and this study for *Ovatella*) found that the pleural ganglia develop from the same anlage as the cerebral ganglion or that both anlagen are intimately connected.

(2) Most of these studies describe a separate origin of the pleural ganglia from an ectodermal proliferation site usually located on the upper side of the foot (e.g. ERLANGER (1892) for *Bithynia*, SMITH (1935) for *Patella*, CROFTS (1937) for *Haliotis*, MORITZ, (1939) for *Crepidula*, CREEK, (1951) for *Pomatias*, D'ASARO (1966, 1969) for *Bursa*, *Distorsio* and *Thais*, HONEGGER (1974) for *Ampullarius*, DEMIAN & YOUSIF (1975) for *Marisa,* GUYOMARC'H-COUSIN (1974) for *Littorina*, THOMPSON (1958) for *Adalaria*, BICKELL & CHIA (1979) for *Doridella*, HENCHMAN (1890) for *Limax* and CUMIN (1972) for *Lymnaea.* In his review on molluscan morphogenesis, RAVEN (1966) assumed that this is the general pattern in gastropods.

(3) GUIART (1899) proposes that pleural ganglia are always formed in connection with the pedal ganglion in gastropods. Recently, PAGE (1992a,b) argues that this is generally true for nudibranchs. She concludes from her study on *Melibe leonina* that cells from separate proliferation zones (placodes) for pleural and pedal ganglia ingress to produce fused pleural and pedal ganglia.

These substantially different descriptions appear to give the impression that the mode of pleural ganglia formation is highly variable and not linked to a specific pattern. However, several reports of a separate origin seem questionable under closer scrutiny. (1) The formation mode of the pedal connectives in *Ovatella myosotis* enables a re-interpretation of certain earlier studies. The fact that the pleuropedal connectives of *Ovatella* are formed prior to the cerebropedal connectives and remain larger than the latter throughout the larval period (Fig. 23) is surprising. It suggests that some authors (e.g. HENCHMAN, 1890; CONKLIN, 1897; KRIEGSTEIN, 1977 (see below); PAGE, 1992a,b (see below)) apparently mistook the pleuropedal connective as the cerebropedal connective. The incorrect interpretation of connectives leads to a false determination of the respective ganglia. (2) Descriptions reporting a separate ectodermal proliferation site for the pleural ganglion are vague and provide no explaining figures. Moreover, some workers admit some doubts on this matter (HENCHMAN, 1890; GUYOMARC'H-COUSIN, 1974). (3) It is generally problematic to identify the path of unlabelled migrating cells, regardless of the histological sectioning technique applied. Attributing an ectodermal proliferation zone (placode) to a forming ganglion becomes more hypothetical the more distantly both structures are located. However, such accounts are the strongest or only evidence for different development, rather than a common origin, of the pleural and cerebral ganglia.

Although data on pleural ganglia formation in gastropods are incomplete and contradictory, they allow speculation on the evolutionary trend of their formation. According to CROFTS' description (1937) of the developing nervous system of *Haliotis*, the pleural ganglia lie next to the pedal ganglia when first visible. The long distance between pleural and cerebral ganglia precludes the formation of the former from a common anlage with the cerebral ganglion in this archaeogastropod. Rather, the pleural ganglia appear to be formed in close association with the pedal ganglia, as observed in another archaeogastropod, *Theodoxus prevostianus* (pers. obs.). This suggests a correlation between the mode of formation and later position of the pleural ganglia. In archaeogastropods the pleural ganglia lie near the pedal ganglia (hypoathroid condition), whereas in other gas-

tropods they (primarily) lie near the cerebral ganglia (epiathroid condition) (a secondary hypoathroid condition as in ellobiids often occurs) (SALVINI-PLAWEN & HASZPRUNAR, 1987; HASZPRUNAR, 1988, 1993). Does the development of the pleural ganglion reflect this condition in that it is formed in association with the pedal ganglion in primitive gastropods and in association with the cerebral ganglion in evolved gastropods? If so, one may generally expect the pleural ganglia to be formed at least in close association with the cerebral ganglia in gastropods with an epiathroid organisation. Most of the data for opisthobranchs and pulmonates correspond to that model. Further observations, in particular on archaeogastropods and caenogastropods, will be needed for a definitive answer. For a discussion of this topic see also HASZPRUNAR (1993).

Pedal commissure:
The literature contains a variety of different accounts of the formation of the gastropod pedal commissures. The outgrowth of nervous fibers from the pedal ganglia was observed in *Littorina* (GUYOMARC'H-COUSIN, 1974) and was similar in *Ovatella*. In *Limax* (HENCHMAN, 1890) and *Haliotis* (CROFTS, 1937) cell outgrowth was observed. In some caenogastropods (MORITZ, 1939; D'ASARO, 1969) the primordium consists of cells closely associated with the overlying ectoderm. These substantially different modes of formation might be explained by the different proportions and developmental sequences of the pedal elements.

Visceral loop:
Previous studies on gastropod visceral loop formation concentrated on the shifting and fusion of complete ganglia (REGONDAUD, 1964; KRIEGSTEIN, 1977). Data on the actual formation of individual elements are scarce.

The information available on the location of the ectodermal placodes of the gastropod visceral loop ganglia differs considerably. In most prosobranchs the placodes are reported to lie near the opening of, or inside, the mantle cavity (SMITH, 1935 for *Patella*; CROFTS, 1937 for *Haliotis*; CREEK, 1951 for *Pomatias*; D'ASARO, 1969 for *Distorsio* and *Bursa*). This probably represents the primitive condition, as in pulmonates (this study for *Ovatella*) and opisthobranchs (PAGE, 1992a for *Melibe*). The reported position of the primordia outside the mantle cavity as in ampullariids (Prosobranchia) (e. g. DEMIAN & YOUSIF, 1975) may be explained by the derived developmental mode of these gastropods (direct development and delayed mantle cavity formation).

The development and organisation of the larval visceral loop of *Melibe* (PAGE, 1992a) resembles that of *Ovatella* in many respects, although Page's interpretations of the "left pallial placode" differs. This structure is closely associated with the "visceral placode". The "left pallial placode" and the "visceral placode" resemble the two portions of the visceral ganglion anlage of *Ovatella*. Page's interpretation may be rooted in her preference for the hypothesis of individual anlagen for all ganglia (p. 359). The above reports of a common anlage of the cerebral and pleural ganglion clearly prove this hypothesis to be incorrect. The account of the late appearance of the "visceral placode" (6 days after shell loss) in *Melibe* (PAGE, 1992a, p. 356) must be erroneous, because elsewhere this structure is figured in an early veliger stage (PAGE, 1992a, fig. 3B).

The developmental mode of the suboesophageal ganglion of *O. myosotis* is remarkable because all previous studies report an individual ectodermal proliferation zone for that ganglion. If the "left pallial placode" of *Melibe* is regarded as part of the visceral ganglion anlage, then the suboesophageal ganglion may be formed in a similar manner as in *Ovatella*.

The newly formed connectives of the gastropod visceral loop have often been reported as bands of cells. They were described either as outgrowths from the ganglia (DELSMAN, 1914; DEMIAN & YOUSIF, 1975) or as formed by the ectoderm located between the forming ganglia (RIEDL, 1960; D'ASARO, 1966, 1969). More recent studies (PAGE, 1992a,b, 1993; this study) found newly formed connectives that consist solely of fibers. This might be due to the much higher resolution of the histological techniques used in this study, suggesting that fibrous connectives may have previously been overlooked.

(d) Comments on previous studies on gastropod nervous system genesis:

KRIEGSTEIN (1977) described the developmental sequence and fusion of ganglia in *Aplysia californica* in detail without, however, particularly focusing on the origin of the pleural ganglia. An examination of his figures (Fig. 1) suggests that what he designated as the "cerebral ganglion" may be the cerebropleural ganglion, and that the first connection between the "cerebral" and pedal ganglion (stage "2") is the true pleuropedal connective. Three indications support this conclusion: (1) JACOB (1984) described a common anlage for cerebral and pleural ganglia in the same species. (2) The angle of the "cerebropedal connective" and its position directly in front of the statocyst in stage "2" is identical to that of the pleuropedal connective in the subsequent stages. (3) A comparison with the corresponding structures of *Ovatella myosotis* (Fig. 23) reveals a remarkable similarity except for the determination of the "cerebral" ganglion and the connective to the pedal ganglion. Kriegstein's interpretation might be due to the fact that he did not examine more stages of the crucial developmental phase between his stages "2" and "3": The detailed examination of exactly this phase led to the different results in *Ovatella*.

JACOB (1984) was the only investigator to use ectodermal cell labeling. Although the study provides decisive support for the widely accepted hypothesis of the ectodermal origin of neurons, the methods may be inappropriate to relate certain proliferation zones to individual forming ganglia. Because Jacob did not specifically label certain ectodermal areas, morphological criteria had to be used to trace individual cells or cell groups. Based on her interpretations, however, this morphological analysis appears to be of limited reliability. For example the structure she designated as "heart" (Figs. 2b, 4b, 5b, 6a; H) is clearly not a heart at all. Furthermore, the presence of cells with internal ciliary bundles (Fig. 8a) is interpreted as indicating ganglia formation from ciliated ectodermal cells. However, only particular epidermal areas like the velar cells or the anterior part

of the foot are ciliated in gastropod veligers: ganglia formation zones are predominantly non-ciliated. The figures in Jacob's study (figs. 3, 4a, 5a) suggest that she mistook velar cells as proliferation zones. An alternative interpretation of the internally ciliated cells in the larval nervous system of *Aplysia* is given by SCHAEFER (1992): they probably represent cells of the cephalic sensory organ of gastropod larvae (see BONAR, 1978; CHIA & KOSS, 1984; UTHE, 1991, 1995). As argued above, the presence of additional lateral proliferation zones for the "cerebral ganglia" (i.e. the cerebral ganglia plus commissure) remains questionable.

The most detailed account on nervous system genesis of gastropods is given by PAGE (1992a,b) for *Melibe leonina*. Unfortunately, interpretation errors led to the striking conclusion that the pleural ganglia are fused with the pedal ganglia throughout development. This conclusion was immediately questioned (HASZPRUNAR, 1993; GOSLINER, 1994; CARROLL & KEMPF, 1994), and in a subsequent paper the author (PAGE, 1993) admitted that her main hypothesis was incorrect. Since details were not provided, it seems necessary to re-examine the model in detail to point out its problems.

In the examined posthatching larval stages, two pairs of connectives were found, projecting ventrally from the "cerebral ganglia" (Fig. 24D). The first-formed pair, which is already present at hatching, was interpreted as the "cerebropedal connectives" and the other one as the "cerebropleural connectives". These interpretations can be disproved by comparative anatomical as well as by embryological evidence. (1) PAGE (1992b) identified the "cerebropedal connectives" because they "...can be identified in all larval and post-larval stages by their association with the statocyst nerves...". This incorrect premise appears to be responsible for the later confusions. In fact, statocysts are typically located adjacent to the pleuropedal connective in gastropods. In adults, the statocysts typically lie partially embedded in the pedal ganglion, posteriorly, adjacent to the junction of the pleuropedal connective and the pedal ganglion (e.g. LEMCHE, 1956, figs. 354, 356; HERSCHLER & DAVIS, 1980, fig. 6; HASZPRUNAR, 1985b, fig. 3, 1985c, fig. 3A). In adult gastropods the pleuropedal connective is therefore much more closely-associated with the statocyst than the cerebropedal connective is.. Although the statocyst nerves always emerge from the cerebral ganglion, the ventral portions of these nerves and those of the pleuropedal connectives are in intimate contact with each other, as in *Ovatella*. The nervous system of *Melibe* (PAGE, 1992b, Fig. 1) shows this typical configuration when interpreted in this manner. (2) Features of the development and organisation of anterior nervous system elements of *Ovatella myosotis* show remarkable similarities with those of *Melibe leonina*: The first formed pair of ventral connectives from the cerebral ganglia contains fibers of the statocyst nerve, is thicker and lies posteriorly to the other pair. Because of these similarities, the homology of the respective connectives seems highly likely. Therefore the designations of the connectives to the pedal ganglion of *Melibe* should be changed as follows: The "cerebropedal connective" of Page represents the pleuropedal connective; the "cerebropleural connective" represents the cerebropedal connective.

Page interpreted the portion of the pedal ganglion which forms the connection to the cerebropedal ("cerebropleural") connective as "pleural ganglion" (Fig. 24D). Based on the revised interpretation, the only possible position for the pleural ganglia is where the pleuropedal connectives merge with the dorsal nervous system portion, the cerebropleural ganglion.

Page herself acknowledged that the position of the pleural ganglion is the most controversial part of her analysis. Her interpretation of a portion of the pedal ganglia as the "pleural ganglia" was mainly based on the positions of ectodermal placodes. She assumed that ingression zones (placodes) on the side of the foot of *Melibe* are homologous with prosobranch and pulmonate ingression zones, which reportedly provide cells for the pleural ganglia. The shortcomings of this deduction are: (1) the limited reliability of previous data for a separate ingression site for pleural neurons (see above); (2) the failure to explain how to trace exactly the ingression path of neurons from distantly located placodes in *Melibe*. Therefore the pleural ganglia of *Melibe* - as in any nudibranch - must be regarded as located in between the cerebral and visceral loop ganglia throughout development.

In another study PAGE (1993) used the developmental sequence of nudibranch nervous system elements for far-reaching considerations on molluscan origin and phylogeny. She applied the neutral terms anterior and posterior pedal connectives for the two pairs of connectives that emerge from the pedal ganglion (Fig. 24E) and stated that the posterior connectives emerge from the visceral loop. As explained above, these connectives obviously represent the cerebropedal (anterior) and pleuropedal (posterior) connectives. The sites of their origin from the dorsal portion of the nervous system mark the position of the respective ganglia, which are usually fused in nudibranchs. Thus, the pleural ganglia are located where the posterior (pleuropedal) connectives emerge. Page neglected to mention the pleural ganglia and left the question of their position open, stating that the posterior connectives emerge from the visceral loop. While this at first seems to contradict the designation of the posterior connective as the pleuropedal connective, the problem may simply involve terminological discrepancies because elsewhere, PAGE (1992a, p. 354), following BULLOCK (1965), regarded the pleural ganglia as part of the visceral loop. Accordingly, the posterior connectives would be construed as emerging from the pleural ganglia. Interpreting the pleural ganglia as part of the visceral loop is unusual because most workers regard the visceral loop as emerging from the pleural ganglia (e.g. FRETTER & GRAHAM, 1962; FRANC, 1968; SCHMECKEL, 1985; HASZPRUNAR, 1985a, 1988; SALVINI-PLAWEN, 1991; herein).

PAGE (1993) also questioned conventional models of molluscan and gastropodan tetraneury. This is based on the interpretation that the pedal cords stem from the visceral loop and not from the circumoesophageal nerve ring. However, if the pleural ganglia are regarded as elements of the circumoesophageal nerve ring, no contradiction to the conventional model of gastropodan tetraneury is recognisable: the first-formed structure is the anterior nerve ring with three pairs of ganglia (which may be partly fused); the visceral loop originates from the pleural ganglia, and the pedal nerves from the pedal ganglia. The late appearance of

the anterior (cerebropedal) connectives fits well into that model as they may represent an additional structure to the primary nerve ring. PAGE'S (1993) model also identified pedal cords in nudibranch larvae, a surprising claim because advanced gastropods such as opisthobranchs usually do not have pedal cords like primitive gastropods and other molluscs. In the pulmonate *O. myosotis*, for instance, neither larval nor adult anatomy allow one of the nerves to be homologized with the archaeogastropod pedal cords. The lack of a convincing justification for the homology of the first-formed pedal nerves of *Melibe* with archaeogastropod pedal cords makes this proposal doubtful.

CHIA & KOSS (1989) and PAGE (1993) detected two pairs of ganglia in the propodium of late stage dorid nudibranch larvae. PAGE (1993) homologized them with structures of the monoplacophoran nervous system. She viewed the "labial ganglia", which may be homologous to the temporary portion of the larval cerebral ganglion in *Ovatella* (see above), as a homologue of the monoplacophoran labial ganglia plus commissure. Although this is an intriguing idea, it requires additional supportive data from the nervous system genesis of primitive gastropods to be confirmed. The homology of the other ("subradular") pair of ganglia with the subradular ganglion of monoplacophorans (PAGE, 1993) is totally unfounded, and the supposedly homologous structure is not even present in monoplacophorans. New detailed investigations on the nervous system in Monoplacophora (HASZPRUNAR & SCHAEFER, 1996a,b; SCHAEFER & HASZPRUNAR, 1996) revealed that they lack a subradular commissure with a true ganglion. I suggest that the two latter structures are a special feature of dorid nudibranchs, representing one of the numerous pairs of accessory ganglia in the head region of adult dorids (WOLTER, 1967) whose formation was accelerated. This phenomenon of adultation (JÄGERSTEN, 1972; GOULD, 1977) - the shifting of adult characters into larvae - is quite common in nudibranchs as external adult features, which are absent in typical opisthobranch larvae, have been reported for a number of veligers. These include rhinophores in *Rostanga* (CHIA & KOSS, 1982); cerrata anlagen in *Melibe* (BICKELL & KEMPF, 1983); shell loss, rhinophores and cerrata anlagen in *Tergipes* (DE NORDMANN, 1846) and *Aegires* (THIRIOT-QUIÉVREUX, 1977). A comparable case of accelerated gangliogenesis in opisthobranchs are the ganglia lying ventrally, adjacent to the cerebropleural ganglia of the *Haminoea* veliger (Fig. 7). Subsequent development reveals these ganglia to be accelerated (= previously formed) ganglia of the labiotentacular nerve (Schaefer, 1992). The homology of the latter with the ganglia in the propodium of dorid nudibranchs seems unlikely due to their distinctly different location ventral to the oesophagus.

KEMPF *et al.* (1987) and CARROLL & KEMPF (1994) provided another interpretation for the location of the pleural ganglion in the larval nudibranch nervous system. They located the pleural ganglia of *Tritonia diomedea* and *Berghia verrucicornis* (Fig. 24C) in the visceral loop, far from the cerebral ganglia. As already suggested by PAGE (1992b) for *Tritonia diomedea*, these ganglia should be interpreted as visceral loop ganglia because of (1) their equal distance to the "cerebral" and the visceral ganglion, (2) their unequal position in the horizontal plane, as is apparent for *Tritonia* and (3) the lack of connectives to the pedal ganglia. What contributed to the interpretation of KEMPF *et al.*. (1987) and CARROLL & KEMPF (1994)? In aeolidiid nudibranchs the connectives from the larval cerebropleural ganglion to the pedal ganglion are extremely close to each other. In the larval *Aeolidiella soemmeringi* (for taxonomy see SCHMECKEL, 1985) the cerebropedal and pleuropedal connectives are separated by a small gap only (TARDY, 1970, fig. 9A) (Fig. 24A). The same arrangement is present in the aeolidiid *Phestilla sibogae* throughout development (pers. obs.). It therefore seems likely that the connection to the pedal ganglion in the aeolidiid *Berghia verrucicornis* in fact represents both the cerebropedal and pleuropedal connective, which CARROLL & KEMPF (1994) were unable to resolve separately. The thickness of the respective structure in the tritoniid *Tritonia diomedea* (KEMPF *et al.*, 1987, fig. 2D) indicates that the same holds true for this species. As a consequence the designation of *Tritonia* and *Berghia* larval nervous system elements should be altered as follows: the "cerebral ganglia" are the cerebropleural ganglia; the "pleural ganglia" are visceral loop ganglia which may represent the sub- and supraoesophageal ganglia.

Figure 24 gives a comprehensive illustration of descriptions of the anterior nervous system components of late stage euthyneuran larvae, pointing out the varying interpretations of elements. It seems important to note that the designation is unmistakable in *Aplysia californica* (Fig. 24B) and *Ovatella myosotis* (Fig. 24F). Only in these species are the pleural ganglia separate in the adult, allowing clear designation of the surrounding elements. Interpretation of larval elements was done by tracing the fate of the elements in question until the adult. I suggest that the comparison of larval stages of other euthyneurans with these species would prove very helpful in designating the elements in question and lead to very similar results, as is the case in *Aeolidiella* (Fig. 24A) and *Haminaea* (Fig. 24F).

It has been shown here that the pleural ganglia lie between the cerebral ganglia and the viscera loop. This general position is supported by descriptions of separate pleural ganglia in some nudibranchs (MAC FARLAND & O'DONOGHUE, 1929; WÄGELE, 1989). Like in other gastropod groups, this ganglion is clearly separated from the cerebral ganglion but connected with this by the cerebropleural connective, and with the pedal ganglion by the pleuropedal connectives. It remains, however, unclear if these ganglia contain portions of visceral loop ganglia.

(e) Sensory organs:

Gastropod eyes and statocysts typically originate from ectodermal invaginations (e. g. *Marisa*: DEMIAN & YOUSIF, 1975; *Ovatella*: herein). The statocyst anlage is generally positioned on the side of the foot, whereas the eye anlage is near the cerebral ganglion.

The static canal of the opisthobranch larva *Rostanga pulchra* (CHIA *et al.*, 1981) is very similar to that of *O. myosotis* in position, organisation and relation to the statocyst nerve, suggesting a homology of the structures. In *O. myosotis*, however, it does not represent the remnant of the statocyst invagination as it was presumed by CHIA et al. (1981) for *R. pulchra*. It is pre-

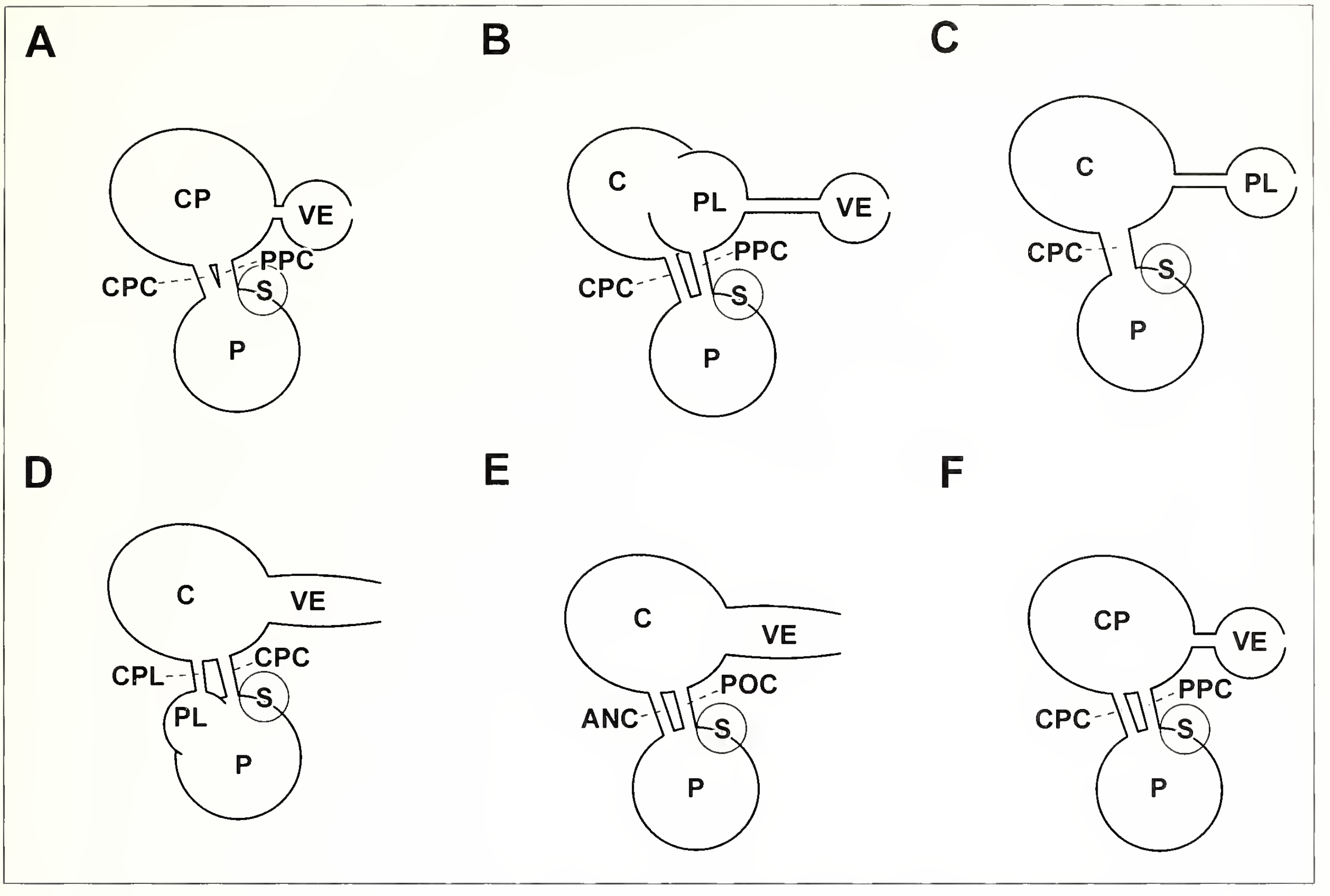


Fig. 24. Diagrammic illustration of descriptions of anterior nervous system elements of late stage euthyneuran larvae. Lateral view from the left. A. *Aeolidiella soemmeringi* (Tardy, 1970, 1974); B. *Aplysia californica* (Kriegstein, 1977); C. *Berghia verrucicornis* (Carroll & Kempf, 1994); D. *Melibe leonina* (Page, 1992a,b); E. *Rostanga pulchra* (Page, 1993); F. *Haminaea navicula* (Schaefer, 1992), *Ovatella myosotis* (herein); ANC = anterior connective; C = cerebral ganglion; CP = cerebropleural ganglion; CPC = cerebropedal connective; CPL = cerebropleural connective; P = pedal ganglion; PL = pleural ganglion; POC = posterior connective; PPC = pleuropedal connective; VE = visceral loop element.

sumably homologous with the duct linking the statocyst and nerve in other adult pulmonates (Kerkut & Walker, 1975). The formation of a single statolith in the larval statocyst and its replacement by statoconia during subsequent development (as in *Ovatella*) has been reported for other gastropods as well (e. g. *Haliotis*: Crofts, 1937; *Onchidella*: Fretter, 1943), suggesting that statoliths represent the more primitive evolutionary condition in gastropods.

The innervation mode of statocysts in adult gastropods is enigmatic. They are intimately connected with the pedal ganglia but innervated from the distant cerebral ganglia. The developmental sequence of the respective structures provides a possible explanation. As in *Ovatella*, the statocyst formation generally precedes that of the pedal ganglion (Moor, 1983). Therefore, the statocysts must be initially innervated from the cerebral ganglia, a condition which is retained throughout development. The intimate connection of the statocyst nerve and the pleuropedal connective near the statocyst apparently represents a remainder of the larval organisation (where the pleuropedal connective and the statocyst nerve emerge from the same nerve trunk).

The transitory osphradium of *O. myosotis* presumably represents a phylogenetic recapitulation of this structure which is lacking in most adult non-aquatic pulmonates. A similar temporary osphradium has been reported in developing stylommatophorans (Pelseneer, 1901: *Helix aspersa*; Henchman, 1890: *Limax maximus*).

The lack of the cephalic sensory organ in *Ovatella* (see formation of the cerebral commissure) is apparently due to the intracapsular development of this species: this organ may be reduced because it has no function during the larval phase inside the egg capsule. The planktotrophic larva of the ellobiid *Laemodonta octanfracta*, on the other hand, bears a well developed cephalic sensory organ with internally located ciliary bundles (pers. obs.). The presence of such an organ in the planktotrophic larva of another pulmonate, the onchidiid *Onchidium branchiferum* (pers. obs.), provides evidence that this is basic pattern in pulmonates. The connection of the cerebral commissure to the epithelium, which persists quite long in *Ovatella*, may be interpreted as a remnant of the cephalic sensory organ.

ACKNOWLEDGEMENTS

I thank L. v. Salvini-Plawen (Vienna), W. F. Ponder (Sydney), G. Haszprunar (Munich), K. Schaefer (Vienna) and M. Haase (Vienna) for critically reading of the manuscript and providing useful comments.

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Lavoro accettato il 2 Ottobre 1998

Bollettino Malacologico, Roma, **34** (1-4): 23-26, [1998]1999 - Società Italiana di Malacologia

Un probabile rappresentante della famiglia Haloceratidae Warén & Bouchet, 1991 nel Pliocene emiliano

Luca Bertolaso & Stefano Palazzi

KEY WORDS: Paleontology, Mollusca, Gastropoda, Haloceratidae, Pliocene, EmiliaRomagna, Italy.

ABSTRACT A new fossil species, *Haloceras contribulis*, is here described. It has been collected in the Pliocene epibathial clay beds of Emilia (NW Italy). Its attribution to the genus *Haloceras* Dall, 1889 is somewhat temptative in reason of a higher number of spiral threads on protoconch II.

RIASSUNTO Ricerche sulla malacofauna pliocenica dei depositi pelitico-argillosi epibatiali dell'Emilia (Italia NO) hanno permesso agli autori di rinvenire 7 esemplari di una nuova specie che, dopo accurati confronti, è stata tentativamente attribuita al genere *Haloceras* Dall, 1889, nonostante la differenza data dal maggior numero di filetti spirali sulla protoconca II.

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INTRODUZIONE

La famiglia Haloceratidae è stata recentemente istituita per un gruppo poco noto di molluschi di profondità, la cui rarità è forse dovuta alla necessità di speciali condizioni trofiche ed edafiche. Le caratteristiche anatomiche, pur con la presenza di caratteri arcaici, avvicinano la famiglia ai Capulidae e ai rappresentanti meno modificati dei Tonnoidea. Per i due generi ad essa attribuiti, *Haloceras* Dall, 1889 e *Zygoceras* Warén & Bouchet,1991, non sono conosciuti ritrovamenti fossili (WARÉN & BOUCHET, 1991). In questo articolo descriveremo alcuni esemplari provenienti dalle argille pelitiche epibatiali del Piacenziano emiliano che, nonostante alcune differenze nell'ornamentazione della protoconca II, ci sembra possano essere attribuiti al primo dei due generi citati.

Haloceras contribulis n. sp.

Descrizione dell' olotipo

Protoconca multispirale di poco più di 2 giri per un diametro di 725 mm; distinta in protoconca I e II (fig.1-4). Protoconca I (osservata al microscopio ottico) a nucleo granuloso, con una estensione di 0,45 di giro e superficie coperta di granuli allineati in senso spirale solo in zona abapicale. Protoconca II molto complessa: inizialmente presenta, in zona abapicale, 3-4 cordoncini spirali a prosecuzione di quelli granulosi della protoconca I; gradualmente si aggiungono altri cordoncini in senso adabapicale fino a essere presenti sull'intera superficie in numero complessivo di 7. Irregolari allineamenti di granuli appaiono dapprima perpendicolari al solo cordoncino sottosuturale; nell'ultimo quarto di giro ricoprono poi tutta la superficie creando una caratteristica zigrinatura data dall'intersezione degli allineamenti variamente orientati. Al termine della protoconca II i cordoncini spirali scompaiono, mentre la zigrinatura arriva fino al labbro prosoclino della conchiglia larvale, che segna, con netto distacco, l'inizio della teleoconca.

Teleoconca troco-rissoiforme, con 3,1 giri convessi, angolati al quarto superiore, alta 4,5 mm e larga 3,5 mm.

Ornamentazione cancellata, con maglie rettangolari allungate in senso spirale alla cui intersezione sono presenti spine ottuse. Coste assiali evidenti, rispettivamente in numero di 13, 12, 15 per giro, debolmente flessuose e prosocline nella fascia suturale, rettilinee o leggermente opistocline adapicalmente. Cordoni spirali principali rilevati, 2 sui primi giri e 3 sull'ultimo, ai quali si accompagna una scultura spirale secondaria costituita da deboli cordoncini sulla rampa suturale e filetti intercordonali che, pur presenti fin dal primo giro, divengono cospicui solo sull'ultimo. Un quarto e meno rilevato cordone spirale principale, sul quale si arrestano le coste assiali, delimita superiormente la base, discretamente declive e ornata da 8-9 cordoncini spirali variamente rilevati, il più interno dei quali borda una fascia liscia leggermente rialzata che contorna il profondo ombelico. Peristoma ovoidale, ristretto anteriormente da una svasatura; labbro esterno incompleto ma, presumibilmente, semplice; labbro interno sottile e rettilineo, leggermente riflesso sull'ombelico.

Variabilità

Nei nostri esemplari il diametro della protoconca varia tra 650 e 725 mm, i filetti spirali della protoconca II si possono presentare in numero da 7 a 10 e, inoltre, l'ornamentazione finale, zigrinata, può variare la sua estensione: ad esempio in un esemplare di Monticelli essa è presente per un piccolo tratto unicamente in zona suturale.

Assetto conchigliare più o meno depresso. Caratteri ornamentali piuttosto variabili: si presentano esemplari con poche coste assiali e con scultura spirale obsoleta, ma sempre corrispondente ai caratteri della specie, ed esemplari in cui i filetti spirali secondari eguagliano i primari (vedi figg. 6-7). Non possediamo tutti i termini di transizione tra i due estremi, ma que-

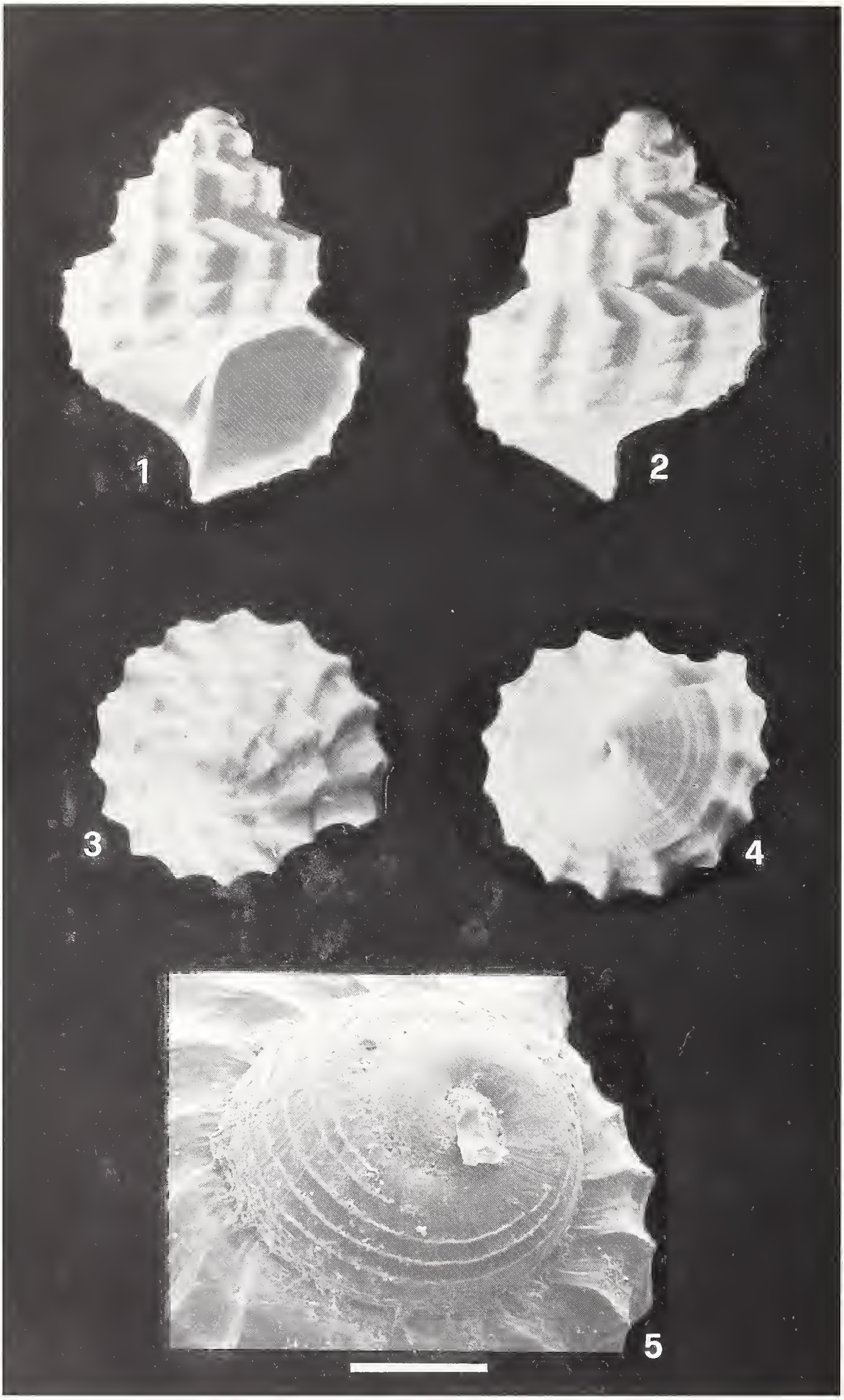


Figure 1-5. *Haloceras contribulis* n. sp., Cava di Campore, Salsomaggiore Terme (PR) (Pliocene). 1-2. Olotipo, altezza 4,5 mm. 3-4. Olotipo, larghezza 3,35 mm. 5. Particolare della protoconca di un esemplare giovanile. Linea di scala 200 µm.

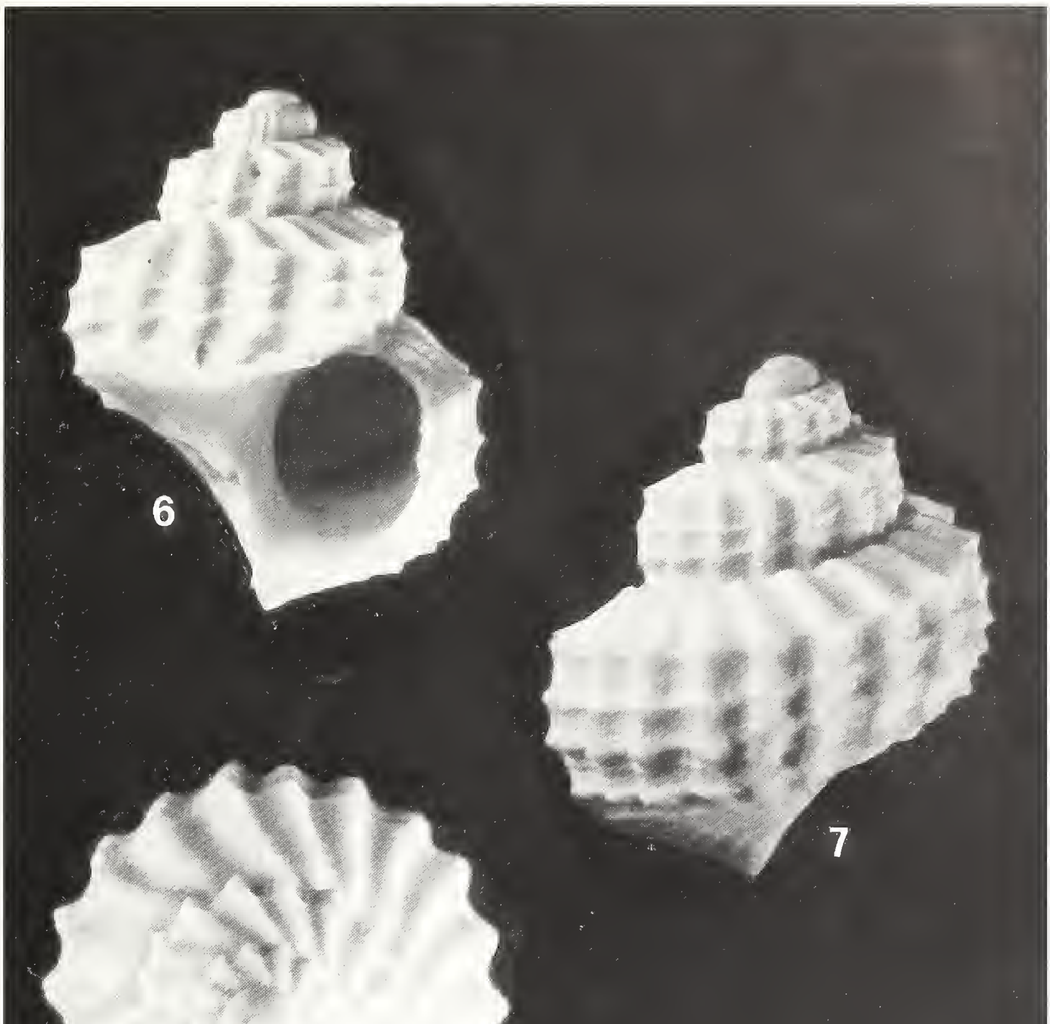


Figure 6-9. *Haloceras contribulis* n. sp., Cava di Campore, Salsomaggiore Terme (PR) (Pliocene). 6-7. Paratipo, altezza 4,05 mm. 8-9. Paratipo, larghezza 3,35 mm.

sto ci sembra imputabile al limitatto numero di esemplari in nostro possesso ed al loro differente stadio di sviluppo.

ORIGINE DEL NOME

Dal latino *contribulis* : appartenente alla stessa tribù.

MATERIALE ESAMINATO

Cava di Campore (*locus typicus)*, Comune di Salsomaggiore Terme (Parma), Pliocene (Piacenziano): 4 esemplari, tutti con protoconca conservata).

Cava di Rio della Moja, Monticelli, Comune di Quattro Castella (Reggio Emilia), Pliocene (Piacenziano): 3 esemplari incompleti di cui 2 con protoconca conservata.

COLLOCAZIONE DEI TIPI

Olotipo depositato presso il Laboratorio di Malacologia dell'Università di Bologna (figg. 1-4).
Paratipo illustrato in coll. Bertolaso, Correggio (RE), (figg. 6-9).
Un paratipo di Campore in coll. Palazzi, Modena.
Altri paratipi in coll. Bertolaso, Correggio (RE).

DISCUSSIONE

Nonostante alcune caratteristiche dell'ornamentazione possano generare dubbi sulla correttezza della collocazione in *Haloceras* Dall, 1889, non abbiamo individuato altri taxa che rispondessero alle peculiarità dei nostri esemplari quanto questo genere. Infatti il tipo di protoconca e l'aspetto conchigliare avvicinano concretamente la nuova specie qui descritta agli appartenenti alla famiglia Haloceratidae Warén & Bouchet, 1991; inoltre tanto le caratteristiche sedimentarie delle località da cui proviene il nostro materiale quanto le rispettive associazioni faunistiche (Raffi & Taviani, 1983; Marasti & Raffi, 1977) concordano con i dati batimetrici noti per i rappresentanti attuali della famiglia.

Haloceras contribulis si discosta dalle specie dell'Atlantico nordorientale sia per i caratteri della teleoconca che della protoconca (Bouchet & Warén, 1993). L'alto numero dei cordoncini spirali della protoconca II la distingue, inoltre, da tutte le altre specie finora descritte (*Zygoceras* e *Haloceras* posseggono rispettivamente 2 e 3 cordoncini spirali sulla conchiglia larvale) ed in particolare modo da *Haloceras phaeocephala* Warén & Bouchet, 1991. Questa specie australiana è l'unica che presenti assetto conchigliare, protoconca ed ornamentazione della teleoconca superficialmente simili alla nostra; inoltre si può rimarcare come ambedue possano presentare individui poco ornamentati. I caratteristici cordoncini spirali della protoconca II di *H. contribulis* sono comunque sufficienti a tenere separate le due specie (Warén & Bouchet, 1991).

Pur riconoscendo che la presenza di 7-10 cordoncini spirali sulla protoconca II è una caratteristica in disaccordo anche con la descrizione della famiglia Haloceratidae, noi crediamo che l'insieme degli altri caratteri sia sufficiente per la collocazione dei nostri esemplari in questa famiglia e, in ragione delle caratteristiche conchigliari, nel genere *Haloceras* Dall, 1889. La possibile descrizione di un nuovo nome generico ci sembra superflua anche per quanto scritto da Warén & Bouchet (1991: 152) relativamente alla ipotetica possibilità di reperire rappresentanti della famiglia con protoconca diversa, di tipo paucispirale. La differenza sopra evidenziata può quindi portare, a nostro credere, solo a un ampliamento concettuale circa la morfologia protoconcale dei taxa coinvolti.

RINGRAZIAMENTI

Desideriamo ringraziare il Dipartimento di Scienze della Terra dell'Università di Milano e il tecnico Agostino Rizzi per le foto al microscopio elettronico a scansione nonchè il sig. Enrico Borghi per le altre gentilmente realizzate.

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Lavoro accettato il 30 Maggio 1998

Bollettino Malacologico, Roma, **34** (1-4): 27-32, [1998]1999 - Società Italiana di Malacologia

Description of a new species of Conidae Fleming, 1822 from the Mediterranean Sea: *Conopleura aliena* n. sp.

Carlo Smriglio, Paolo Mariottini & Sergio Calascibetta*

KEY WORDS: *Conopleura aliena* n. sp., Conidae, Mediterranean Sea.

ABSTRACT A new species of Conidae Fleming, 1822 is here described from the Mediterranean Sea: *Conopleura aliena* n. sp. Two shells of the new species have been dredged from two distinct geographical areas of the Tyrrhenian Sea and collected from two different kind of marine zones. In particular, the first specimen from a bathyal muddy bottom surrounding a deep-sea coral bank located in the Central Tyrrhenian Sea; the second one from a circalittoral soft bottom located off the coast of Sicily, Southern Tyrrhenian Sea. The systematic position of the new taxon is tentatively assigned to the family Conidae, subfamily Mangeliinae Fischer, 1884, genus *Conopleura* Hinds, 1844, according to the recent revision of the superfamily Conoidea (= Toxoglossa) Rafinesque, 1815 proposed by TAYLOR *et al.* (1993).

RIASSUNTO Viene proposta una nuova specie di Conidae Fleming, 1822 per il Mar Mediterraneo: *Conopleura aliena* n. sp. Il taxon è descritto solo sulla base dei caratteri conchigliari di due esemplari provenienti da due diverse zone geografiche con differenti tipologie di fondale. Un esemplare è stato dragato da un fondale batiale fangoso circostante una biocenosi a coralli bianchi nel Mar Tirreno Centrale; il secondo è stato raccolto su un fondale del piano circalitorale, a substrato fangoso, della costa siciliana settentrionale (Mar Tirreno Meridionale). Il nuovo taxon, che per le peculiari caratteristiche morfologiche non è avvicinabile a nessuna specie conosciuta per il Mar Mediterraneo e l'adiacente Oceano Atlantico, è stato inserito nella famiglia Conidae, tentativamente nella sottofamiglia Mangeliinae Fischer, 1884, in accordo all'ultimo lavoro di revisione della superfamiglia Conoidea (= Toxoglossa) Rafinesque, 1815 proposto da TAYLOR *et al.* (1993). In questa sottofamiglia è posizionato anche il genere *Conopleura* Hinds, 1844, con la specie tipo *Conopleura striata* Hinds, 1844, originariamente descritta per l'area Indo-Pacifica. Questo sembra essere un genere adatto ad ospitare al momento il nuovo taxon, in particolare la struttura del seno anale di *C. aliena* mostra una forte somiglianza con quello di *C. striata*. Vengono inoltre elencate le conchiglie trovate assieme alla nuova specie nei due diversi ritrovamenti.

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INTRODUCTION

In the frame of a study carried out in the past years with the aim to characterize the bathyal assemblages from the Central Tyrrhenian Sea, off the Latium coast (Italy) (SMRIGLIO *et al.*, 1996), we have been continuing the investigation on the molluscan fauna occurring in the deep-sea coral and muddy-bathyal communities ("biocoenose des coraux blancs, CB" and "biocoenose des vases bathyales, VB": PÉRÈS & PICARD, 1964) of this area. Several interesting and poorly known species belonging to the family-group Turridae H. & A. Adams, 1853 *s. l.* have been reported from the dredged material so far examined (SMRIGLIO *et al.*, 1987a, 1987b, 1988). During the sorting of a sample collected in 1987 from the muddy-bathyal bottoms of this area, we screened a very peculiar shell that could not be identified among the known Mediterranean species. At that time, Dr Philippe Bouchet (Muséum national d'Histoire naturelles, Paris), kindly answering to our request of identification pointed out the relationship between some morphological characters of this specimen and the ones present in the Indo-Pacific genus *Conopleura* Hinds, 1844 (*in litt.* 20-12-1988). In May 1997, a second specimen of this still unidentified species was collected off Sicilian coast, dredged at a depth of 105 m from a muddy bottom. This individual is smaller and was found within a glass bottle. This second finding has prompted us to describe in this paper the species *Conopleura aliena* n. sp. as new to science. Because the new taxon is only known from shells, it is conservatively placed within the family Conidae, subfamily Mangeliinae Fischer, 1884, genus *Conopleura* Hinds, 1844, according to the classification proposed by TAYLOR *et al.* (1993). We are aware that without anatomical information the new taxon described has only provisional position, but we think that at present no definitive systematic statement can be made even at the family rank in this very complicated group of molluscs.

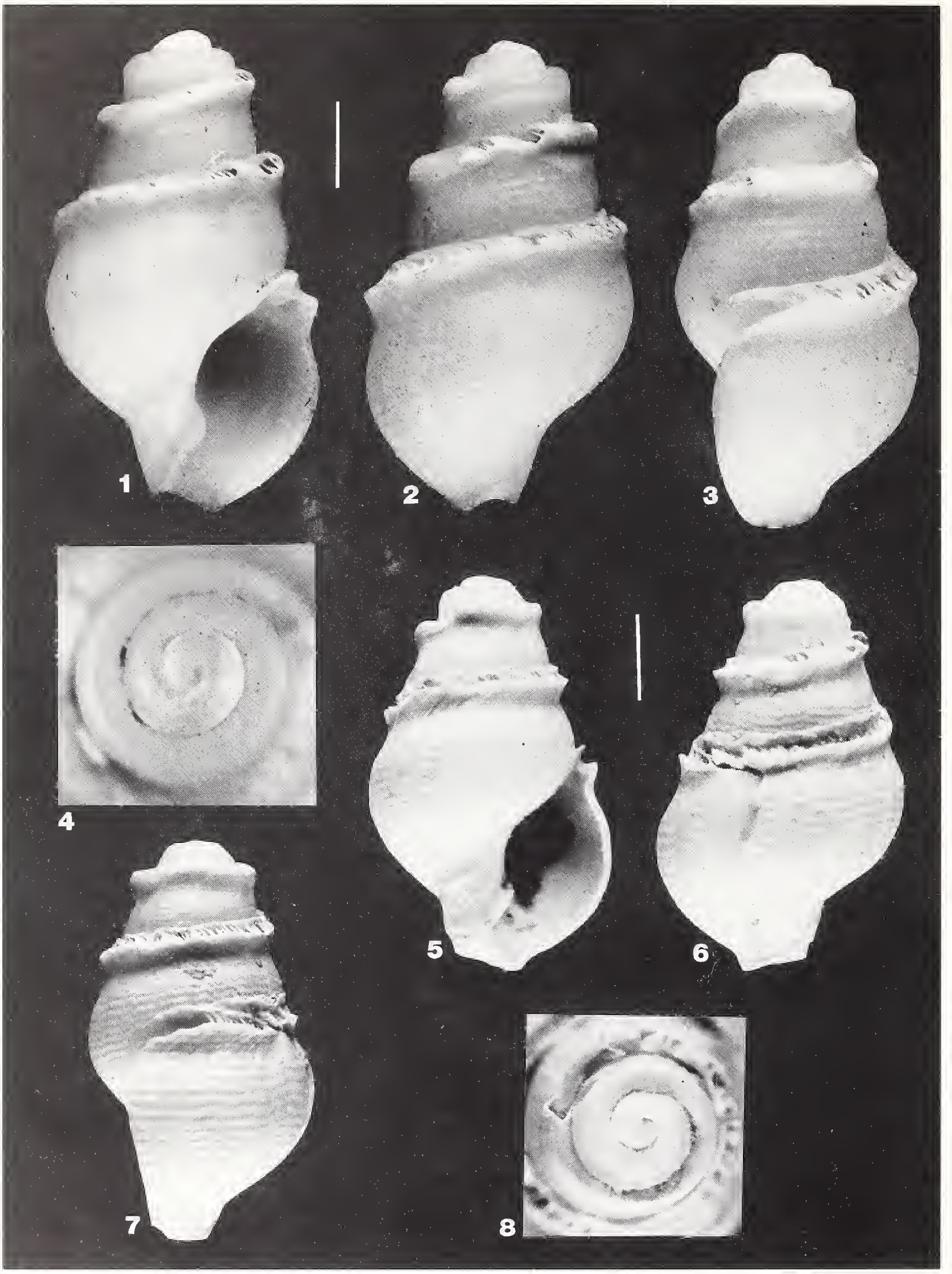
SYSTEMATICS

Superfamily	Conoidea	Rafinesque, 1815
Family	Conidae	Fleming, 1822
Subfamily	Mangeliinae	Fischer, 1883
Genus	*Conopleura*	Hinds, 1844
Species	*Conopleura aliena*	n. sp.

Conopleura aliena n. sp. (Figs. 1-8)

Type material

Type material of *C. aliena* consists of two empty shells. The holotype, 6.8 x 4.0 mm, from Central Tyrrhenian Sea (41°51'N - 011°28'E), 350 m depth, collected from a muddy-bathyal bottom (*sensu* PÉRÈS & PICARD 1964) surrounding a deep-sea coral



Figures 1-4. *Conopleura aliena* n. sp. Holotype. Frontal, dorsal and lateral views, and particular of the protoconch. 6.8 x 4.0 mm. Central Tyrrhenian Sea (41°51'N;11°28'E), 350 m depth. MZB collection (Italy). Scale bar is 1.0 mm for figs 1-3. Figures 5-8. *Conopleura aliena* n. sp. Paratype. Frontal, dorsal and lateral views, and particular of the protoconch. 5.0 x 3.5 mm. Southern Tyrrhenian Sea, off Isola delle Femmine (PA), Sicily, 105 m depth. Private collection of S. Calascibetta, Palermo (Italy). Scale bar is 1.0 mm for figs 5-7.

bank, is deposited in the malacological collection of the Museo di Zoologia dell'Università di Bologna (MZB), Italy, with the number 12694. The paratype, 5.0 x 3.5 mm, from Southern Tyrrhenian Sea (off the Isola delle Femmine, Palermo), 105 m depth, found within a glass bottle collected from a muddy circalittoral bottom, is deposited in the private collection of Sergio Calascibetta, Carini (PA), Italy.

Description

Shell small, light, turriculate, slender posteriorly. Protoconch paucispiral intorted of one whorl, smooth, almost planospiral, without microsculpture. Teleoconch of four and a half whorls, slightly convex, body profile gradate, sculpture consisting of numerous wavy and equally spaced spiral striae, crossing the few and faint axial growing lines, which are irregularly distributed. Suture strong and pronounced, anal sinus sutural and very deep, with the sulcus only partially obliterated during the shell development; where the sulcus is not completely sealed along the body whorls, a sort of lamellate scar is clearly evident. Aperture narrow, sigmoid-shaped, about half of the entire height, siphonal canal short. Peristome convex and sinuous with an evident columellar rib, outer lip thin. Umbilicus absent. Colour whitish, uniform and semi-matt. Animal unknown.

Etymology

The specific name *aliena*, which means in Latin extraneous, refers to the peculiar shell shape never observed before in any genus of the family occurring in the Mediterranean Sea.

Type locality

Central Tyrrhenian Sea, 41°51'N - 011°28'E.

Distribution

Only known from the Central and Southern Tyrrhenian Sea, and showing a range of batymetry from 100 to 350 m.

REMARKS

The "Revision of the northeast Atlantic bathyal and abyssal Turridae" by BOUCHET & WARÉN (1980) allows a cohemprensive view of the species of the family Turridae *s. l.* normally occurring below 300 m of depth in the North-East Atlantic Ocean and in the Mediterranean Sea. In that work, we could not find any species resembling the new taxon proposed. Furthermore, we have been unable to find *C. aliena* neither in the literature analyzed and referring to the Recent (DALL, 1889; DAUTZENBERG & FISCHER, 1896; LOCARD,1897; NORDSIECK, 1968, 1973, 1977; DI GERONIMO & PANETTA, 1973; DI GERONIMO, 1974; CURINI-GALLETTI, 1977; WARÈN, 1980; TERRENI, 1981; MOSQUERA, 1983; BOGI, 1986; CECALUPO & GIUSTI, 1986; CARCASSI, 1987; BOUCHET & TAVIANI, 1989; SABELLI *et al.*, 1990, 1992; GIRIBET & PENAS, 1997; RÓLAN *et al.*, 1998) and fossil (CERULLI-IRELLI, 1910; MALATESTA, 1974; CAPROTTI, 1976; RINDONE & VAZZANA, 1989; VAZZANA, 1991; CAVALLO & REPETTO, 1992; FERRERO & MERLINO, 1992; BONFITTO *et al.*, 1994; CHIRLI, 1997) species of the family Turridae *s. l.*, nor in the collections of Recent and fossil Mediterranean and Atlantic shells, that we have had the chance to examine so far. As suggested by Dr Philippe Bouchet (Muséum national d'Histoire naturelles, Paris; *in litt.* 20-12-1988) and in our opinion, the monotypic Indo-Pacific genus *Conopleura* Hinds, 1844, (type species *Conopleura striata* Hinds, 1844), is a taxon in which the new species can be at least provisionally placed. In fact, there is a strong similarity in the lamellate sculpture of the anal sinus between the two shells. On the contrary, the teleoconch shapes, the apertures and the spiral sculptures are quite different, as well as the shapes, sculptures and number of the protoconch whorls. A specimen of *Conopleura striata* Hinds, 1844, dredged off Bohol, Philippines, has been figured for comparison (Figs. 9-11). We think worth quoting the description by POWELL (1966) on the shell of *Conopleura*: *"Shell small, 8.2 mm., broadly biconical, resembling Eucithara in a general way but with several peculiar features. The shoulder sulcus is a series of deep pits, separated by thin radiating lamellae, the effect when viewed from above being like the spokes of a wheel. The axial sculpture is lyrate, in the form of broadly rounded flattened flexuosus axials, which rise above the lower edge of the shoulder concavity, giving a serrated or coronated effect. The whole surface is crossed by a very distinctive type of spiral sculpture which is in the form of vavy obloque lirations, which widely diverge as the whorls increase. The aperture is narrow and sinuous, terminating in a short unnotched canal, and there is a slight false umbilicus. The outer lip is thin and has a deep narrow and oblique subsutural sinus, which is constricted at is entrance by a massive parietal callus pad. Colour dull white or buff. Range - New Guinea in 7 fathoms (Type) and near the south coast of Timor in 34 metres".*

The prosobranch gastropod superfamily Conoidea (=Toxoglossa), shows extreme diversity, according to the recent classification proposed by TAYLOR *et al.* (1993) includes six families. Among these, the family Conidae, which in turn has been subdivided into seven subfamilies, offers a suitable allocation for the new taxa. In particular, the subfamily Mangeliinae, which contains the genus *Conopleura*, has several shell diagnostic features matching the ones of *C. aliena* (TAYLOR *et al.*, 1993). In particular, the small shell size, the presence of a deep labial sinus on the shoulder, siphonal canal short and the protoconch smooth (in the case of of *C. aliena* the paucispiral protoconch indicates a non-planktotrophic larval development). Since the new taxon is described only on shell characters, we prefer conservatively assigned it to pre-existing high order groups, at present tentatively placing *C. aliena* in the genus *Conopleura*. At the mean time, the extreme uniqueness of the shell morphology shown by *C. aliena*, has prompted us to describe it as a new species in spite of the absence of any anatomical data. At first glance, the general shape of the two shells under investigation resembles the one of a nassariid, the possibility that these teleoconchs are the same teratological form of some mediterranean bathyal nassariid sp. has been taken into account. We think that, besides the obvious presence of the subsutural sinus-slit, the overall sculpture and the smooth protoconch of *C. aliena* are not comparable to the ones shown by the only nassariid, *Nassarius lima* (Dillwin, 1817) (Figs. 12-14), normally occurring at that depth in the Mediterranean Sea and, in fact, present in the malacofauna found together with *C. aliena*. In particular, the



Figures 9-11. *Conopleura striata* Hinds, 1844. Frontal and lateral views, and particular of the protoconch. 16.5 x 8.0 mm. Bohol (Philippines). Private collection of L. Bozzetti, Milano (Italy). Scale bar is 2.0 mm for figs 9-10. Figures 12-14. *Nassarius lima* (Dillwin, 1817). Frontal view, particulars of the protoconch and teleoconch sculpture. 9.5 x 5.3 mm. Central Tyrrhenian Sea (41°51'N;11°28'E), 350 m depth. Scale bar is 1.0 mm for fig. 12.

sculpture of *N. lima* is consisting of equally spaced strong axial ribs, crossed by equally spaced pronounced spiral cordelets, which confer a reticulated looking to the shell surface. At a higher magnification, it can be observed that the spacing among the axial ribs are filled by tiny axial striae (Fig. 14). On the contrary, the teleoconch sculpture of *C. aliena* shows only wavy and equally spaced spiral striae crossing faint axial growing lines. Since the apex morphology shown by *C. aliena* is not the one of a typical turrid, the possibility that the real protoconch whorls may have been lost, exposing a domed internal callous plug, is not ruled out. In spite of the fact that in nassariids the protoconch erosion/plug formation is a common phenomenon, we have never observed something similar to that in *N. lima*. On the other hand, if apex lost is a "normal" event during the growth of *C. aliena*, its systematics could be dramatically changed according to the observation of the real protoconch.

We have identified shells of several other mollusc species found with *C. aliena* that are worthy to list. Those occurring with the holotype and collected from the bathyal zone of the Central Tyrrhenian Sea are: *Propilidium exiguum* Thompson, 1843, *Lepetella* cf. *laterocompressa* (De Rayneval & Ponzi, 1854), *Emarginula tenera* Locard, 1892, *Clelandella miliaris* (Brocchi, 1814), *Danilia otaviana* (Cantraine, 1835), *Putzeysia wiseri* (Calcara, 1842), *Alvania cimicoides* (Forbes, 1844), *Alvania subsoluta* (Aradas, 1847), *Orbitestella dariae* (Liuzzi & Stolfa Zucchi, 1979), *Trophon muricatus* var. *barvicensis* (Johnston, 1825), *Nassarius lima* (Dillwin, 1817), *Amphissa acutecostata* (Philippi, 1844), *Granulina gofasi* Smriglio & Mariottini, 1996, *Gymnobela abyssorum* (Locard, 1897), *Microdrillia loprestiana* (Calcara, 1841), *Pleurotomella demosia* (Dautzenberg & Fischer P., 1896), *Pleurotomella gibbera* Bouchet & Warén, 1980 ex Jeffreys ms., *Teretia teres* (Reeve, 1844), *Heliacus alleryi* (Seguenza G., 1876), *Mathilda cochlaeformis* Brugnone, 1873, *Japonacteon pusillus* (McGillivray, 1843), *Asperarca nodulosa* (Müller, 1776), *Chlamys bruei* (Payraudeau, 1826) and *Cadulus subfusiformis* (Sars M., 1865). Those occurring with the paratype and collected from the circalittoral zone of the Southern Tyrrhenian Sea are: *Lepetella* cf. *laterocompressa* (De Rayneval & Ponzi, 1854), *Alvania cimicoides* (Forbes, 1844) and *Cadulus subfusiformis* (Sars M., 1865). We point out that these species are also present in the taphocoenosis found with the holotype. In conclusion, we think that *C. aliena* is a rare species and at present its records are limited to the Tyrrhenian Sea (Fig. 15), further findings of this species are needed to clarify its systematic position and its occurrence in all the Mediterranean basin.

ACKNOWLEDGEMENTS

We would like to express our gratitude to Dr Philippe Bouchet (Musèum national d'Histoire naturelles, Paris, France) for correspondence concerning the taxonomic problem of *C. aliena*. We are really grateful to Dr Marco Oliverio (Dipartimento di Biologia, Università di Roma Tre, Italy) and two anonymous reviewers for their critical comments and advice on the present paper. We are very indebted to Dr Antonio Bonfitto (Museo di Zoologia dell'Università di Bologna, Italy) for generously providing references. Sincere thanks are due to Dr Luigi Bozzetti (Milano, Italy) for the loan of *C. striata* from his collection. We furthermore thank Mr Maurizio Imperato, Mr Claudio Imperato and Mr Giannandrea Bulgarini for technical assistance.

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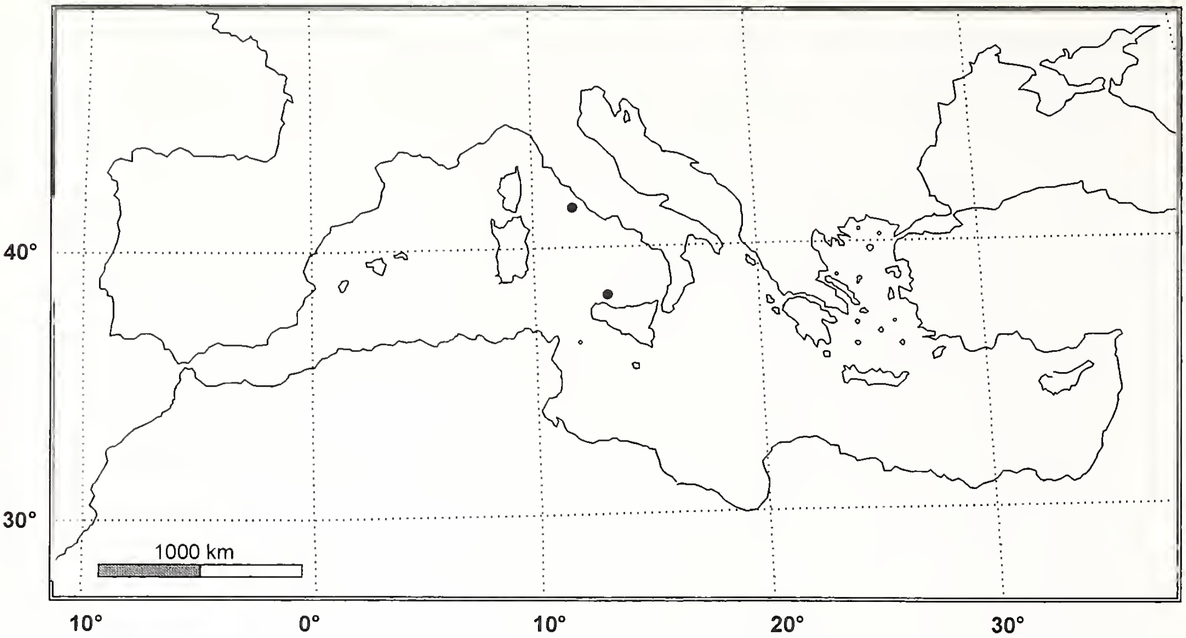


Figure 15. Records of *Conopleura aliena* n. sp. (●) in the Mediterranean Sea.

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Lavoro accettato il 2 Ottobre 1998

Pleistocene and Recent Mediterranean species of *Granulina* (Gastropoda, Marginellidae), with description of four new species

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KEY WORDS: *Granulina*, Marginellidae, systematics, new species, Mediterranean, Pleistocene, Recent.

ABSTRACT Eleven species of *Granulina* Jousseaume, 1888 are reported from the Mediterranean Quaternary: *G. rosarioi* n. sp., *G. jhomisensis* n. sp., *G. ovulina* (Monterosato, 1891), *G. tenuilabiata* n. sp., *G. occulta* (Monterosato, 1869), *G. marginata* (Bivona, 1832), *G. boucheti* Gofas, 1992, *G. minusculina* (Locard, 1897), *G. gofasi* Smriglio & Mariottini, 1996, *G. guttula* n. sp. and *G. melitensis* Smriglio, Mariottini & Rufini, 1998.

Six species are Pleistocene to Recent, i.e. *G. tenuilabiata* n. sp., *G. occulta, G. marginata*, *G. boucheti*, *G. minusculina* and *G. gofasi*, while *G. jhomisensis* n. sp., *G. ovulina* and *G. rosarioi* n. sp., are only known from the Pleistocene. Two species, *G. melitensis* and *G. guttula* n. sp., are only known as Recent species. Main evolutionary trends of *Granulina* in the Mediterranean are: colonisation of the outer shelf and the upper slope, endemicity and high speciation rate.

RIASSUNTO Per il Quaternario del Mediterraneo sono riportate undici specie del genere *Granulina* Jousseaume, 1888, quattro delle quali nuove: *G. rosarioi* n. sp., *G. jhomisensis* n. sp., *G. ovulina* (Monterosato, 1891), *G. tenuilabiata* n. sp., *G. occulta* (Monterosato, 1869), *G. marginata* (Bivona, 1832), *G. boucheti* Gofas, 1992, *G. minusculina* (Locard, 1897), *G. gofasi* Smriglio & Mariottini, 1996, *G. guttula* n. sp. e *G. melitensis* Smriglio, Mariottini & Rufini, 1998. *G. rosarioi* n. sp. e *G. jhomisensis* n. sp. sono note solo per il Pleistocene, la prima per depositi di piattaforma profonda della Sicilia sud-occidentale, la terza per depositi superficiali della Sicilia sud-orientale. *G. tenuilabiata* n. sp. è specie epibatiale nota per il Pleistocene della Calabria meridionale e per una stazione al largo della Sardegna orientale, probabilmente di età würmiana. *G. guttula* n. sp. è nota solo per una stazione al largo dell'Isola di Ponza (Tirreno centrale) ad 84 m. Per il Pleistocene vengono riportate anche *G. minusculina*, *G. marginata*, *G. boucheti*, *G. gofasi* e *G. ovulina*; per quest'ultima viene designato il lectotipo. Uniche specie francamente superficiali (infralitorali) sono *G. marginata*, *G. boucheti* e *G. jhomisensis* n. sp., nessuna delle quali, comunque, mostra particolari affinità verso le specie del vicino Atlantico. Fra le altre specie sembrano riconoscibili dei gruppi, cioè il gruppo *rosarioi-ovulina-guttula-occulta*, il gruppo *gofasi-tenuilabiata* ed il gruppo *melitensis-minusculina*. Il primo gruppo ha distribuzione tipicamente circalitorale, mentre gli altri due hanno distribuzione più profonda, ma solo *G. minusculina* ha distribuzione francamente batiale.

Alcuni problemi restano aperti, ed in particolare il significato tassonomico di una forma pleistocenica che sembra rappresentare il ceppo dal quale *G. marginata* e *G. boucheti* si sono differenziate nel corso del Quaternario. Le principali tendenze evolutive del genere *Granulina* nell'area Mediterranea sono rappresentate da tendenza a colonizzare ambienti della piattaforma profonda ed epibatiali, spiccata endemicità e veloce tasso di speciazione.

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INTRODUCTION

The genus *Granulina* Jousseaume, 1888 includes small ovate, colourless and smooth-shelled "marginelliform" gastropods. The last whorl envelopes the previous ones, the lip is thickened, inflected and usually denticulate. Four columellar plications and a parietal callus are present. As stressed by Gofas (1992), species identification needs careful examination of shell shape, lip, denticles, columellar plications, etc. In the present work, a diagnostic value is also stressed for the parietal callus.

Traditionally included in Marginellidae Fleming, 1828 (e.g. Coan, 1965; Gofas, 1992), *Granulina* was recently transferred to Cystiscidae Stimpson, 1865 by Coovert & Coovert (1995). Marginellidae and Cystiscidae prove to be not as closely related as previously thought, the former sharing instead relations to Volutidae and the latter to Olividae (Coovert & Coovert, 1995). Anyway, there is not fully agreement about the allocation of *Granulina* in Cystiscidae (S. GOFAS, pers. com.). *Granulina* has a simple bifurcate head ("Type 2 animal" of Coovert & Coovert, 1995), strongly pointing to the Marginellidae. The "modified cystiscid internal whorls", mostly resorbed, of *Granulina* [which led Coovert & Coovert (1995) to rise the subfamily Granulininae] may be convergent to Cystiscidae due to the small size of the genus. Coovert & Coovert (1995) also stressed radular peculiarities of *Granulina*, but no other anatomical information is available. At present, the move of *Granulina* to Cystiscidae seems not well supported and the allocation in Marginellidae is then maintained.

The Eastern Atlantic and Mediterranean species of *Granulina* were reviewed by Gofas (1992), who checked four species from the Mediterranean (excluding Gibraltar), i.e. *G. marginata* (Bivona, 1832), *G. boucheti* Gofas, 1992, *G. occulta* (Monterosato, 1869) and *G. minusculina* (Locard, 1897). A fifth Mediterranean species, *G. gofasi*, was described by Smriglio & Mariottini (1995) and a sixth one, *G. melitensis*, by Smriglio *et al.* (1998). The European species of *Granulina* were previously accounted by Van Aartsen *et al.* (1984), Contreras (1987) and Muñiz Solis (1987). Bouchet & Warén (1985) reported *Granulina* from the Northeast Atlantic deep waters.

Little is known about the fossil Mediterranean species. The past records of two species from the Plio-Pleistocene, i.e. *G. clandestina* (Brocchi, 1814) and *G. occulta* (Monterosato, 1869), prove to be mostly based on incorrect interpretations of these species and on a general poor knowledge of this genus (see Gofas, 1992).

MATERIAL AND METHODS

Descriptive terminology and morphometry is mainly based on Gofas (1992) and Coovert & Coovert (1995). Descriptions and measurements are based on full-grown specimens. The examined Recent material consists all of empty shells. The following abbreviations are used:

L = shell length
D = shell maximum diameter
L/D = length to maximum diameter ratio
Ld = distance of maximum diameter from anterior ending
Ld/L = relative position of maximum diameter
sh(s) = shell(s)
coll. = collection
UPMC = University Paleontological Museum, Catania
ZMR = Zoological Museum, Rome.

SYSTEMATIC ACCOUNT

Class Gastropoda Cuvier, 1797
Order Neogastropoda Thiele, 1929
Family Marginellidae Fleming, 1828

Genus *Granulina* Jousseaume, 1888

Type-species

Marginella pygmaea Issel, 1869 (by monotypy)

Granulina rosarioi n. sp.
Figs. 1-3

Type material

Holotype and 2 paratypes (both partly broken). UPMC.

Type locality

Pleistocene deep-shelf silts cropping out along the Belice River valley ("Case Catarinicchia"), southwestern Sicily.

Etymology

Named for the author's father, Rosario.

Description

Shell ovoid-elongate (L/D 1.46-1.50), outline well rounded. Posterior rostration well defined. Maximum diameter posterior to half shell length (Ld/L 0.63-0.65). Siphonal notch very weak. Lip markedly thickened, posteriorly bevelled; denticles well defined. Parietal callus narrow, making a deep and wide sinus on body-whorl. Aperture narrow. Four notably broad columellar plications, the uppermost two weaker. Surface smooth, polished. Holotype: L 3.07 mm, D 2.10 mm. Paratypes: L 3.10-3.15 mm, D 2.05 mm.

Distribution

Only known from the type locality. *G. clandestina* and *G. occulta*, formerly listed from this locality (Di Geronimo *et al.*, 1994, tab. 2), now prove to be *G. rosarioi* and *G. gofasi*. Silts are overlaid by shallow-shelf coarse beds, which yielded *G. marginata* and *G. boucheti*.

Remarks

G. rosarioi is somewhat similar to *G. gofasi*. In the former the lip is thicker and bevelled ("labre biseauté" of Gofas, 1992) and the posterior rostration is sharper. The broad columellar plications are also distinctive to *G. rosarioi*.

Granulina jhomisensis n. sp.
Figs. 29-32

Type material

Holotype and 11 paratypes (one subadult, 6 juveniles). UPMC.

Type locality

Pleistocene shallow-shelf muddy-sandy beds cropping out near Còmiso ("Cartiera Mulino"), along the Ippari River valley, southeastern Sicily.

Other examined material

Grammichele ("Catallarga"), southeastern Sicily, Pleistocene, 1 sh.

Etymology

Named from *Jhomisus*, ancient name of Còmiso.

Description

Shell ovoid-elongate (L/D 1.47-1.56), outline weakly rounded. Posterior ending rather truncated. Maximum diameter well posterior to half shell length (Ld/L 0.70-0.71). Siphonal notch distinct. Lip moderately thickened; denticles well defined. Aperture narrow. Four columellar plications, strongly doubled into an outer and an inner series. Outer plications partly merged to form a zigzag, the uppermost two weaker. Surface polished, smooth. Parietal callus wide, making a shallow sinus on body-whorl and an axial ridge almost inside aperture. Holotype: L 2.71 mm, D 1.84 mm. Paratypes: L 2.56-2.71 mm, D 1.82-1.64 mm.

Distribution

The type material comes from fine-grained beds, rich in small-sized molluscs (mainly rissoids and *Bittium*), for which a shallow-water bottom sheltered by *Posidonia oceanica* grasses is inferred (Costa, 1989). The single shell from Grammichele comes from shallow-water coarse beds (see La Perna, 1997).

Remarks

Due to its elongate shape, *G. jhomisensis* appears similar to *G. occulta*. The former differs mainly by a less slender shape, a well distinct posterior slope-break, a more bevelled lip and by being almost non-rostrated. An ill-defined sulcus makes the columellar folds strongly doubled, as known for other species (see Gofas, 1992, p. 4).



Figures. 1-3. *Granulina rosarioi* n. sp. Belice River valley, Pleistocene. 1, 2. Holotype, 3.07x2.10 mm. 3. Paratype, 3.10x2.05 mm (oral side broken). Figures. 4-6. *Granulina gofasi* Smriglio & Mariottini, 1996. Belice River valley, Pleistocene. 4. 3.01x1.99 mm. 5,6. 2.98x2.04 mm. Figs. 7-9. *Granulina gofasi* Smriglio & Mariottini, 1996. Off Lazio coast, 550 m. 7, 8. 2.64x1.88 mm. 9. 2.68x1.82 mm. Figures. 10, 11. *Granulina tenuilabiata* n. sp. Vallone Catrica, Pleistocene. Holotype, 3.43x3.05 mm. Figures. 12. *Granulina tenuilabiata* n. sp. Off eastern Sardinia, 1281-330 m. 2.30x2.05 mm. Figures. 13-16. *Granulina guttula* n. sp. Off Isola di Ponza, 84 m. 13, 14. Holotype, 1.92x1.26 mm. 15, 16. Paratype, 2.13x1.38 mm. Figures. 17. *Granulina* sp. A. Vallone Catrica, Pleistocene. 2.71x1.71 mm.

Granulina ovulina (Monterosato, 1891)
Figs. 43, 44

Gibberulina ovulina Monterosato, 1891: p. 4.

Examined material

Ficarazzi (Palermo), northwestern Sicily, Pleistocene, 145 shs. Lectotype designated by C. Smriglio & R. La Perna (May 1998). ZMR, Monterosato coll., 15/5-17197/A.

Description

Shell ovoid-elongate (L/D 1.63-1.65), outline rounded. Maximum diameter posterior to half shell length (Ld/L 0.65-0.67). Posterior rostration weak. Siphonal notch very weak. Lip thickened; denticulations well developed. Parietal callus hardly distinct, narrow, making a wide and deep sinus on body-whorl. Aperture narrow. Four strong columellar plications. Surface polished, smooth, with ill-defined growth striae. Lectotype: L 3.30 mm, D 2.10 mm. Largest specimen: L 3.80 x D 2.30 mm.

Distribution

Only known from the original material. The Ficarazzi beds contain Pleistocene deep-shelf faunas with scarce epibathyal species (see Di Geronimo & La Perna, 1997: p. 417

Remarks

Gibberulina ovulina was reported as a fossil from Ficarazzi (Palermo) by Monterosato (1891), with a brief and vague description: "Bellissima forma del gruppo della *G. occulta* ma assai più grande" [A very nice form of the *G. occulta* group, but much larger]. *G. ovulina* is indeed rather similar to *G. occulta*, but markedly larger and more inflated. Due to its size, *G. ovulina* appears notably similar to *G. tenuilabiata* n. sp., but the two species differ in several respects: *G. tenuilabiata* is more inflated and rostrated than *G. ovulina*, the lip is notably thicker, less arched and slightly bevelled posteriorly, the aperture is narrower and with well developed denticulations.

The date of *G. ovulina* is labelled as "1896" (Fig. 45), but this was probably due to a misspelling for "1891".

Granulina tenuilabiata n. sp.
Figs. 10-12

Type material

Holotype. UPMC.

Type locality

Epibathyal muddy beds cropping out at Vallone Catrica, southern Calabria, Pleistocene.

Other examined material

Off eastern Sardinia, BS78/2, 41°51'.03N, 10°34'.06E, 1281-330 m, 1 sh. UPMC.

Etymology

Latin *tenuilabiatus* (= thin-lipped), due to its comparatively thin lip.

Description

Shell ovoid-elongate (L/D ca. 1.50), outline well rounded. Maximum diameter posterior to half shell length (Ld/L 0.60). Posterior rostration moderate. Siphonal notch absent. Lip weakly thickened; denticulations faint to lacking. Parietal callus hardly distinct, narrow, making a wide and deep sinus on body-whorl. Aperture rather wide. Four columellar plications, the uppermost two weaker. Surface polished, smooth, with ill-defined growth striae. Holotype: L 3.43 mm, D 2.30mm.

Distribution

Pleistocene to "Recent" (see below), epibathyal. Paleodepths within 500-600 m are inferred for the type-locality beds (Di Geronimo & La Perna, 1997).

Remarks

The single shell from off Sardinia is old looking and might come from Würmian (Latest Pleistocene) beds, as suggested by the molluscan assemblage occurring in the sample. It only differs from the holotype by being smaller and with a comparatively thinner lip, lacking denticulations (faint denticulations are anteriorly present in the holotype). It is difficult to find a very close matching between fossil and Recent forms of *Granulina*, and no reason other than size can be found to keep this shell distinct from *G. tenuilabiata*.

Granulina occulta (Monterosato, 1869)
Fig. 27

Marginella occulta Monterosato, 1869: p. 17, fig. 10.
Volutella parvulina Locard, 1897: p. 126, pl. 21, figs. 3-5.
Granulina occulta (Monterosato) - Gofas, 1992: p. 12, figs. 11 (lectotype), 12, 27.

Examined material

Off southeastern Sicily, PS81/10C, 36°43'.48N, 15°11'.30E, 61-58 m, 3 shs. UPMC.

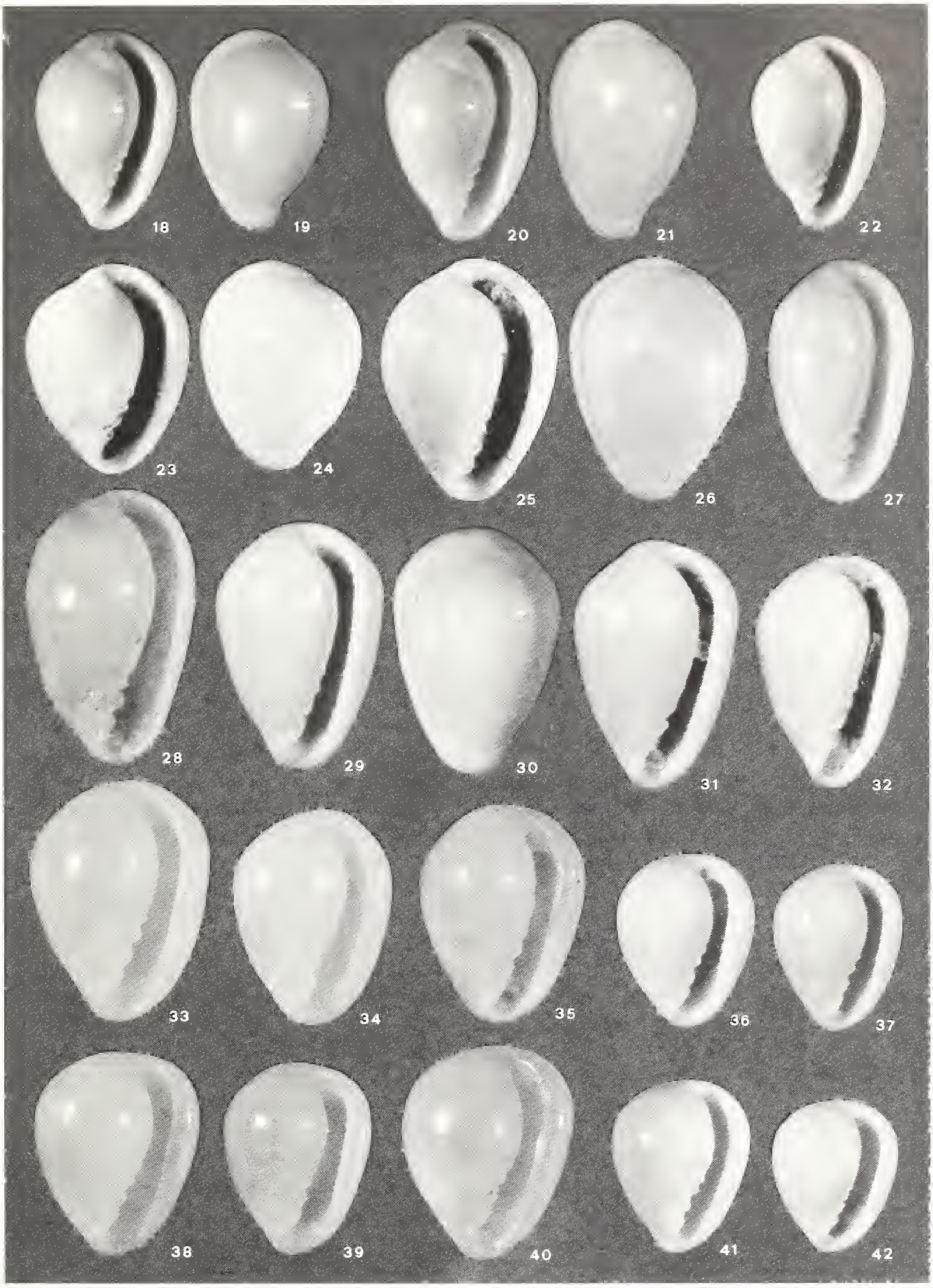
Distribution

G. occulta was described from off "Palermo, 50 m". It is a mid- to deep-shelf species, in Mediterranean and Ibero-Moroccan Gulf (Gofas, 1992).

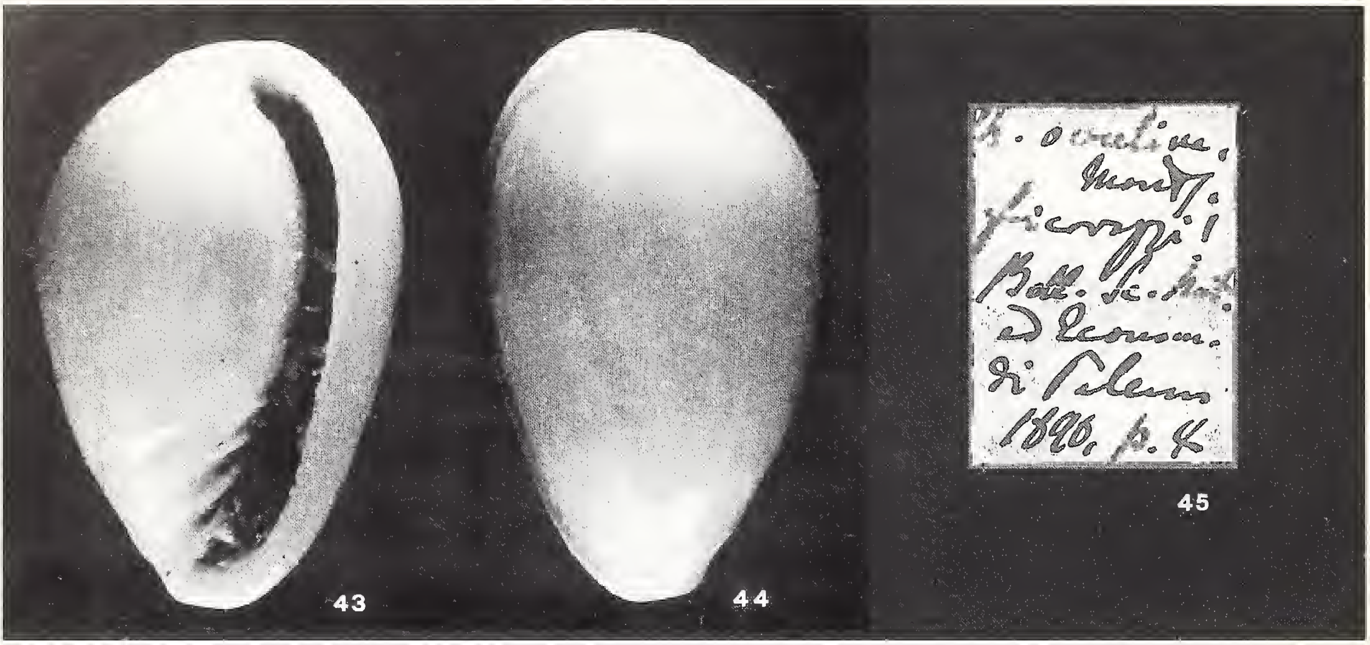
Monterosato (1872, 1877) recorded this species as a fossil from Monte Pellegrino and Ficarazzi (Palermo) and a lot of 60 shells from "Monte Pellegrino" (labelled by Brugnone) is present in ZMR (C. Smriglio, pers. com.).

Remarks

G. occulta has a markedly slender shell, compared with the other species. The callus makes a wide and deep sinus on the body-whorl. Lip denticulations are weakly developed.



Figures 18-22. *Granulina melitensis* Smriglio, Mariottini & Rufini, 1998. Off southeastern Sicily, 200 m. 18, 19. 2.10x1.52 mm. 20, 21. 2.32x1.62 mm. 22. 2.01x1.40 mm. Figures 23, 24.*Granulina minusculina* (Locard, 1897). Aeolian Archipelago, 248 m. 2.21x1.73 mm. Figures 25, 26. *Granulina minusculina* (Locard, 1897). Furnari, Pleistocene. 2.54x1.87 mm. Figure 27. *Granulina occulta* (Monterosato, 1869). Off southeastern Sicily, 61-58 m. 2.52x1.50 mm. Figure 28. *Granulina* sp. B. Off eastern Sardinia, 1281-330 m. 2.83x1.77 mm. Figures 29-32. *Granulina jhonisensis* n. sp. Ippari River valley, Pleistocene. 29, 30. Holotype, 2.71x1.84 mm. 31. Paratype, 2.73x1.82 mm. 32. Paratype, 2.50x1.70 mm. Figures 33, 34. *Granulina boucheti* Gofas, 1992. Acitrezza, 24-38 m. 33. 2.50x1.88 mm. 34. 2.22x1.66 mm. Figure 35. *Granulina boucheti* Gofas, 1992. Grammichele, Pleistocene. 2.27x1.72 mm. Figures 36, 37. *Granulina* cf. *boucheti* Gofas, 1992. Ippari River valley, Pleistocene. 36. 1.80x1.44 mm. 37. 1.75x1.36 mm. Figs. 38, 39. *Granulina marginata* (Bivona, 1832). Acitrezza, 24-38 m. 38. 2.11x1.72 mm. 39. 2.00x1.55 mm. Figure 40. *Granulina marginata* (Bivona, 1832). Grammichele, Pleistocene. 2.22x1.77 mm. Figures 41, 42. *Granulina* cf. *marginata* (Bivona, 1832). Ippari River valley, Pleistocene. 41. 1.80x1.44 mm. 42. 1.61x1.33 mm.



Figures 43, 44. *Granulina ovulina* (Monterosato, 1891), lectotype. Ficarazzi (Palermo), Pleistocene. 3.30x2.10 mm. Monterosato coll. (ZMR). Fig. 45. Original label of *Gibberulina ovulina* Monterosato, 1891.

The synonymy between *Marginella occulta* Monterosato and *Volutella parvulina* Locard was proved by GOFAS (1992), but the rostrated and thick-lipped specimen from off Morocco (1,713 m) reported by BOUCHET & WARÉN (1985, fig. 711) as *G. parvulina* (Locard) seems a distinct Atlantic species.

Some deep-water shells from off eastern Sardinia (BS78/2, 41°51'.03N, 10°34'.06E, 1,281-330 m) are similar to *G. occulta*, but larger (up to 2.85 mm in length), more inflated (L/D ca. 1.60) and with a thinner well-arched lip, without denticulations (Fig. 29). Shells appear as old as as *G. tenuilabiata* from the same station. The taxonomic status of this material is not understood (a deep-water ecotype of *G. occulta*?) and it is tentatively referred to as *Granulina* sp. B.

Granulina marginata (Bivona, 1832)

Figs. 38-40

Volvaria marginata Bivona, 1832: p. 24, pl. 3, fig. 5.
Granulina marginata (Bivona) - Gofas, 1992: p. 6, figs. 5-8, 25.

Examined material

Grammichele ("Catallarga"), southeastern Sicily, Pleistocene, 14 shs. Belice River valley, southwestern Sicily ("Case Catarinicchia"), Pleistocene, 3 shs. Ippari River valley ("Cartiera Mulino"), southeastern Sicily, Pleistocene, 21 shs (*G.* cf. *marginata*). Off Acitrezza, eastern Sicily, SCUBA-diving samples, 24-38 m, 179 shs. Acitrezza harbour (beach), 21 shs. Brucoli, southeastern Sicily, *Posidonia* "mattes", 1-2 m, 8 shs. UPMC.

Distribution

G. marginata is widespread in the western and eastern Mediterranean, in shallow waters (GOFAS, 1992; KOUTSOUBAS *et al.*, 1997). GOFAS (1992), who examined and illustrated the material from Grammichele first, proved the occurrence in the Pleistocene.

Remarks

See under *G. boucheti*.

Granulina boucheti Gofas, 1992

Figs. 33-35

Granulina boucheti Gofas, 1992: p. 10, figs. 9-10, 26.

Examined material

Grammichele ("Catallarga"), southeastern Sicily, Pleistocene, 7 shs. Belice River valley, southwestern Sicily ("Case Catarinicchia"), Pleistocene, 5 shs. Ippari River valley ("Cartiera Mulino"), southeastern Sicily, Pleistocene, 163 shs (*G.* cf. *boucheti*). Off Acitrezza, southeastern Sicily, SCUBA-diving samples, 24-38 m, 39 shs. Acitrezza harbour (beach), 16 shs. Brucoli, southeastern Sicily, *Posidonia* "mattes", 1-2 m, 23 shs. UPMC.

Distribution

G. boucheti was described from Acitrezza and reported from other localities in Sicily, as well as from Corsica, Tunisia, Algeria (GOFAS, 1992) and the Aegean Sea (KOUTSOUBAS *et al.*, 1997). It occurs in shallow waters, often together with *G. marginata*, but less commonly (GOFAS, 1992).

GOFAS (1992) first proved its occurrence in the Pleistocene, on material from Grammichele.

Remarks

The closeness of *G. boucheti* to *G. marginata* was stressed by GOFAS (1992), who noted orange spots on the foot, the base of tentacles and the inner mantle of *G. boucheti* (while these anatomical parts are colourless in *G. marginata*). Conchologically, *G. marginata* is a little smaller and broader (L 1.80-2.30 mm, L/D 1.20-1.31) than *G. boucheti* (L 1.90-2.55 mm, L/D 1.25-1.36). *G. marginata* is also more truncated posteriorly, and with a slightly bevelled lip. Same values of Ld/L are recorded for both species (0.65-0.69). In both species, the callus is notably wide, but not very distinct, and forms a thin ridge almost inside the aperture. The columellar folds are moderately doubled.

While the Pleistocene shells from Grammichele (Figs. 35, 40) and from the Belice River valley, all from shallow-water beds, match the Recent shells of *G. boucheti* and *G. marginata*, the abundant material from the Ippari River valley (same outcrop as for *G. jhomisensis*) is puzzling. Shells are all notably small (L 1.50-1.82 mm, D 1.20-1.45 mm), and most of them (ca. 87%) are slightly less truncated and more elongate (L/D 1.25-1.29) than the few remaining ones (L/D 1.20-1.29). The former group (Figs. 36, 37) is tentatively referred to as *G.* cf. *boucheti* and the latter as *G.* cf. *marginata* (Figs. 41, 42). It should be also noted that the columellar folds are strongly doubled in both groups, while they are slightly to moderately doubled in the Recent shells of both species. The Ippari River valley deposits are probably older than the Grammichele and the Belice River valley ones. The taxonomic status of the Ippari River material is still unclear. It might represent an ancestral form from which both *G. marginata* and of *G. boucheti* became more and more distinct in shape and size through the Quaternary. This could be better understood when other material, possibly from the Pliocene, will be available.

Granulina minusculina (Locard, 1897)

Figs. 23-26

Volutella minusculina Locard, 1897: p. 127, pl. 21, figs. 6-8.
Granulina minusculina (Locard) - Gofas, 1992: p. 16, figs. 15, 16.

Examined material

Furnari, northeastern Sicily, Pleistocene, 2 shs and fragments. Aeolian Archipelago, Southern Tyrrhenian, Eoucumm95 st. 37, 38°29'.33N, 15°50.31E, 248 m, 1 shs. UPMC.

Distribution

G. minusculina is known from the Atlantic (Ibero-Moroccan Gulf) and the Mediterranean (Western Basin), at bathyal depths (down to ca. 1,300 m) (GOFAS, 1992).

The undetermined *Granulina* listed by DI GERONIMO & LA PERNA (1997, tab. 1) from the bathyal Pleistocene of Furnari is *G. minusculina* (Figs. 25, 26). Depths close to 1,000 m are inferred for this deposit.

Remarks

G. minusculina is characterised by a markedly inflated shell, with an almost central maximum diameter (Ld/L ca. 0.58). As noted by GOFAS (1992), denticles extend slightly to the outer surface of the lip.

The examined Pleistocene shells in these respects, but they are slightly larger and more egg-shaped than the Recent ones.

G. occulta of BOUCHET & WARÉN (1985, figs. 713) is *G. minusculina*, as noted by GOFAS (1992).

Granulina gofasi Smriglio & Mariottini, 1996

Figs. 4-9

Granulina gofasi Smriglio & Mariottini, 1996: p. 55, figs. 1ab, 2-8.

Examined material

Belice River valley (locality "Case Catarinicchia"), south-western Sicily, Pleistocene, 2 shs. Off Lazio coast, 550 m (ex C. Smriglio coll.), 5 shs. Off eastern Sardinia, BS78/2, 41°51'.03N, 10°34'.06E, 1,281-330 m, 4 shs. UPMC.

Distribution

G. gofasi was described from 300-600 m in the Central Tyrrhenian Sea (off Lazio coast). For the fossil record, see under *G. rosarioi*.

Remarks

G. gofasi is characterised by a marked egg shape and a well arched posterior lip. Size is up to ca. 3.0 mm in length and 2.0 mm in diameter, L/D 1.44-1.53 and Ld/L ca. 0.65. The two Pleistocene specimens differ from the Recent one by being slightly larger, the lip almost lacking in denticulation (it is faint in the Recent material), and the shape more egg-shaped.

Granulina guttula n. sp.

Figs. 13-16

Type material

Holotype and 18 paratypes (one badly broken, one subadult). UPMC.

Type locality

Off Isola di Ponza, eastern Tyrrhenian, 40°52'.23N, 12°55'.85E, 84 m.

Etymology

Latin diminutive of *gutta* (= drop), due the drop-shaped shell.

Description

Shell ovoid-elongate (L/D 1.48-1.55), outline rounded. Posterior rostration well-defined. Maximum diameter posterior to half shell length (Ld/L 0.62-0.67). Siphonal notch distinct. Lip moderately thickened, posteriorly bevelled; denticulations

	P	R	distribution
Granulina rosarioi n. sp.	+		deep shelf
Granulina jhomisensis n. sp.	+		shallow shelf
Granulina ovulina (Monterosato, 1891)	+		deep shelf
Granulina tenuilabiata n. sp.	+	(+)	epibathyal
Granulina occulta (Monterosato, 1869)	+	+	shelf/(epibathyal)
Granulina marginata (Bivona, 1832)	+	+	shallow shelf
Granulina boucheti Gofas, 1992	+	+	shallow shelf
Granulina minusculina (Locard, 1897)	+	+	bathyal
Granulina gofasi Smriglio & Mariottini, 1996	+	+	deep shelf/epibathyal
Granulina guttula n. sp.		+	deep shelf
Granulina melitensis Smriglio, Mariottini & Rufini, 1998		+	deep shelf

Table. 1. Species of *Granulina* occurring in the Pleistocene (P) and in the Recent (R) Mediterranean, with the ecological distribution.

faint but well defined. Aperture narrow. Four indistinctely doubled columellar plications. Surface smooth, polished. Parietal callus narrow. Holotype: L 1.92 mm, D 1.26 mm. Paratypes: L 1.91-2.25 mm, D 1.28-1.45 mm.

Distribution

Only known from the type locality.

Remarks

G. guttula appears rather similar to *G. occulta*. The former has a more bevelled lip and is markedly inflated posteriorly. It can be also distinguished from *G. melitensis* by being more slender and by lacking the thick posterior callus.

A fossil shell (Fig. 17) from Vallone Catrica (same outcrop as for *G. tenuilabiata*) looks rather similar to *G. guttula* (and to *G. rosarioi* as well), but it is notably larger and with a more central maximum diameter. It might be an undescribed species, but the available material is too scarce to attempt its interpretation. It is referred to as *Granulina* sp. A.

Granulina melitensis Smriglio, Mariottini & Rufini, 1998

Figs. 18-22

Granulina melitensis Smriglio, Mariottini & Rufini, 1998: p. 53, Figs. 1-7.

Examined material

Off southeastern Sicily: PS81/4B, 36°54'.67N, 15°11'.60E, 76 m, 2 shs.; PS81/4C, 36°54'.17N, 15°12'.20E, 95-86 m, 4 shs; PS81/4X, 36°57'.32N, 15°19'.32E, 102-93 m, 3 shs; PS81/2XB, 36°56'.80N, 15°20'.00E, 126-120 m, 3 shs.; PS81/5X, 36°56'.57N, 15°21'.12E, 160 m, 1 sh.; 10P, 38°42'.88N, 15°17'.44E, 200 m, 13 shs. UPMC.

Distribution

G. melitensis was described on shells from 100-120 m in Gnejna Bay, Malta, and was also reported from the Central Tyrrhenian in 250 m (previously as *G. minusculina*: Smriglio & Mariottini, 1996, figs. 4a,b). The living specimen reported by Mifsud (1996: fig. 18) from Malta as *G. minusculina* is *G. melitensis* (S. Gofas, pers. com.). Also *G. occulta* of Bouchet & Warén (1985: fig. 712) from off south-western Sicily is *G. melitensis*. It is rather commonly found on deep-shelf (70-250 m) muddy-sandy bottoms.

Remarks

G. melitensis has a thick posterior callus, sometimes making almost a shallow "tubercle". None of Mediterranean and Eastern Atlantic species shows such a feature. This species differs from *G. minusculina* mainly by being less inflated, less "rhomboidal" in shape and with a fairly well distinct siphonal canal. Further, some soft-part features make the two species well distinct (S. Gofas, pers. com.).

DISCUSSION

Eleven species of *Granulina* are proved to occur in the Quaternary Mediterranean (Tab. 1). Six of the eight extant species range back to the Pleistocene, namely *G. tenuilabiata*, *G. occulta*, *G. marginata*, *G. boucheti*, *G. minusculina* and *G. gofasi*. Three species, i.e. *G. rosarioi*, *G. jhomisensis* and *G. ovulina* are only known from the Pleistocene, while *G. guttula* and *G. melitensis* are only known as Recent species.

Granulina clandestina (Brocchi, 1814), a Pliocene species, deserve some comments. Gofas (1992) faced with Brocchi's species identity proposing a neotype. Coovert & Coovert (1995: p. 74) disagreed with Gofas' interpretation, remarking some discrepancies between Brocchi's figure (1814, p. 642, pl. 15, fig. 11) and Gofas' neotype (1992, p. 5, fig. 3). Although the Pliocene species of *Granulina* are too poorly-known to face critically this problem, *G. clandestina sensu* Gofas was probably present in the Pleistocene too as

CERULLI-IRELLI's record (1911, p. 281, pl. 21, figs. 9-14) of *Cryptospira clandestina* (from Early Pleistocene beds: see BONADONNA, 1968) seems to be based on this species.

A poorly known Pleistocene deep-water species from southern Calabria, *Marginella ovulaeformis* G. Seguenza, 1879 also needs some comments. The original description and drawing (SEGUENZA, 1879: p. 253, pl. 16, fig. 12) suggest a large *Granulina* (ca. 5 mm in length), but the examination of topotypic material (L. Seguenza coll., UPMC; LA PERNA, in prep.) leads to exclude such an allocation, because of the size, the elongate-pyriform shape, the smooth and not inflected lip. A preliminary allocation could be in the marginellid *Ovaginella* Laseron, 1957 (see COOVERT & COOVERT, 1995).

The diversification of *Granulina* in the Mediterranean and its trend to occupy the deep shelf and the upper slope are remarkable. None of the three shallow-water species (*G. marginata*, *G. boucheti* and *G. jhomisensis*) seems to be markedly close to the shallow-water extra-Mediterranean ones (including Gibraltar), i.e. *G. vanhareni* (Van Aartsen, Menkhorst & Gittenberger, 1984), *G. torosa* Gofas, 1992, *G. guancha* (d'Orbigny, 1840), *G. mauretanica* Gofas, 1992 (see GOFAS, 1992). Although *G. jhomisensis* differs notably in shape from *G. marginata* and *G. boucheti*, two features are anyway shared between them, i.e. the wide parietal callus and the apertural callose ridge. *G. tenuilabiata*, *G. gofasi*, *G. rosarioi*, *G. ovulina*, *G. occulta*, *G. melitensis* and *G. guttula* range, as a whole, from the outer shelf to the upper slope, while *G. minusculina* is the sole truly bathyal species. Some of these species, i.e. *G. rosarioi*, *G. ovulina*, *G. guttula* and *G. occulta* seem to form a distinct morphological group with outer-shelf distribution. *G. gofasi* and *G. tenuilabiata* also seem rather close to each other, and both have a deeper distribution. *G. minusculina* clearly belong to a distinct lineages, owing to the squat shape and the lip denticulations extending slightly to the outside (soft-part differences were also reported by GOFAS, 1992). *G. melitensis* is morphologically similar to *G. minusculina* and might represent an "intermediate" form between this species and the outer-shelf group.

G. occulta and *G. minusculina* are the sole species spreading into the Ibero-Moroccan Gulf (GOFAS, 1992), while most species, including the extra-Mediterranean ones have narrow to endemic geographical distribution. Slow gene flow and high speciation rate (probably due to non-planktotrophic larval development) are suggested by this distribution pattern and by the differences between Pleistocene and Recent populations outlined in the present work.

CONCLUDING REMARKS

Some aspects of *Granulina* in the Quaternary Mediterranean remain open; particularly the taxonomic status of the deep-water forms tentatively referred to as *Granulina* sp. A and *Granulina* sp. B, and that of the small Pleistocene form referred to the *marginata-boucheti* complex. Further studies on Plio-Quaternary material will surely help to clear up these problems, as well as to achieve a better knowledge of *Granulina* in the Mediterranean.

ACKNOWLEDGEMENTS

I wish express my thanks to Dr Carlo Smriglio, who helped greatly in many ways, to Dr Serge Gofas, for suggestions during the work, to Dr Eugene Coan and Dr Tiziano Cossignani for help in bibliography, to Prof Italo Di Geronimo and Dr Antonietta Rosso for useful comments and suggestions. I also thank the reviewers Dr Serge Gofas and Dr Marco Oliverio, who greatly aided in improving the manuscript.
Work supported by MURST grants (Di Geronimo, 60%,40%).

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Notes added in proof

While the present paper was in press, additional material was examined. Some of it is worth of being reported.

1. *G. melitensis*. Grammichele ("Ciaramitaio", southeastern Sicily), Pleistocene deep-shelf silts, 3 shs. This species is thus proved to range back to the Pleistocene. 2. *G.* cf. *occulta*. Mineo (southeastern Sicily), Pleistocene, 22 shs (De Fiore coll., UPMC). Shells are notably larger (up to 3.4 mm) than the Recent ones. 3. *G. ovulina*. Grammichele ("Catallarga", southeastern Sicily), Pleistocene shallow-water sands, 1 sh.

Lavoro accettato il 27 Novembre 1998

Bollettino Malacologico, Roma, **34** (1-4): 43-49, [1998]1999 - Società Italiana di Malacologia

El complejo *Brachycythara biconica* (C. B. Adams, 1850) (Mollusca: Gastropoda: Turridae) en Cuba, con la descripción de una nueva especie

Emilio Rolán & José Espinosa

KEY WORDS: Mollusca, Gastropoda, Turridae, *Brachycythara*, new species, Cuba.

ABSTRACT The *Brachycythara biconica* (C. B. Adams, 1850) complex (Mollusca: Gastropoda: Turridae) in Cuba, with the descriptions of a new species. The species of the genus *Brachycythara* found in Cuba are estudied. Four species are differenciated: three of them were previously known: two as species, *B. biconica* (C. B. Adams, 1850) and *B. barbarae* Lyons, 1972; one more, *B. alba* (C. B. Adams, 1850) was hiterto considered a simple variety of *B. biconica*, but it is a valid species; the fourth one is new species and it is described in the present work. Photographs of the shell, protoconch and microsculpture of the species studied are shown.

RIASSUNTO Il complesso di *Brachycythara biconica* (C. B. Adams, 1850) (Mollusca: Gastropoda: Turridae) a Cuba, con la descrizione di una nuova specie - Sono studiate le quattro specie del genere *Brachycythara* rinvenute nell'ambito della revisione dei molluschi di Cuba. Tre di questi taxa erano già conosciuti per l'Atlantico occidentale tropicale. Due erano accettati come specie valide: *Brachycythara biconica* (C. B. Adams, 1850) e *Brachycythara barbarae* Lyons, 1972; l'altro era considerato una varietà - *alba* (C. B. Adams, 1850) - di *B. biconica*, da cui si distingue per le dimensioni della protoconca. La quarta specie, *Brachycythara multicinctata* sp. n., è descritta nel presente lavoro: si differenzia da *B. biconica* principalmente per la taglia minore, la differente microscultura e colorazione; da *B. alba* differisce per la differente microscultura e per la protoconca di dimensioni minori. *B. barbarae* si distingue da tutte le specie del gruppo in quanto manca della microscultura. Abbiamo denominato questo gruppo di specie come "complesso di *Brachycythara biconica*", non tanto per indicare possibili relazioni filogenetiche nel gruppo, quanto per indicare la specie a più ampia distribuzione nei Caraibi (*sensu* Warmke y Abbott, 1961), il taxon più antico e citato in letteratura: probabilmente le altre specie sono state spesso confuse con essa sia in qualche citazione bibliografica che in varie collezioni. Le specie sono illustrate al SEM (conchiglia intera, protoconca e microscultura).

RESUMEN Se estudian las especies encontradas en Cuba pertenecientes al género *Brachycythara*. Se diferencian cuatro especies, de las cuales, tres ya eran previamente conocidas: dos como especies, *B. biconica* (C. B. Adams, 1850) y *B. barbarae* Lyons, 1972; una más, *B. alba* (C. B. Adams, 1850), era considerada una simple variedad de *B. biconica*, pero es una especie válida; la cuarta especie es nueva y se describe en el presente trabajo. Se muestran fotografías al MEB de la concha, protoconcha y microescultura de todas las especies estudiadas.

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INTRODUCCIÓN

Durante el trabajo de revisión de los moluscos de Cuba se han encontrado, en el genero *Brachycythara* Woodring, 1928, cuatro especies de las que tres son extremadamente similares entre sí ("especies crípticas" *sensu* Knowlton, 1986).

Tres son los taxones de este género conocidos en el Atlántico occidental tropical. De ellos, dos a nivel específico: *Brachycythara biconica* (C. B. Adams, 1850) y *Brachycythara barbarae* Lyons, 1972; otro taxon fue descrito como una variedad, *B. biconica* var. *alba* (C. B. Adams, 1850).

A este conjunto de especies le hemos denominado "complejo *Brachycythara biconica*", no como indicador de las posibles relaciones filogenéticas del grupo, las cuales se desconocen, sino por ser esta especie la que, aparentemente, tiene una distribución más amplia en el Caribe (*sensu* Warmke y Abbott, 1961), es el taxon más antiguo y citado en la literatura y, probablemente, las otras especies han sido designadas, en algún momento, con este nombre.

ABREVIATURAS EMPLEADAS:

IDO	Instituto de Oceanología, La Habana
MCZ	Museum of Comparative Zoology, Cambridge
MNCN	Museo Nacional de Ciencias Naturales, Madrid
CER	colección E. Rolán, Vigo
CFG	colección R. Fernández Garcés, Cienfuegos

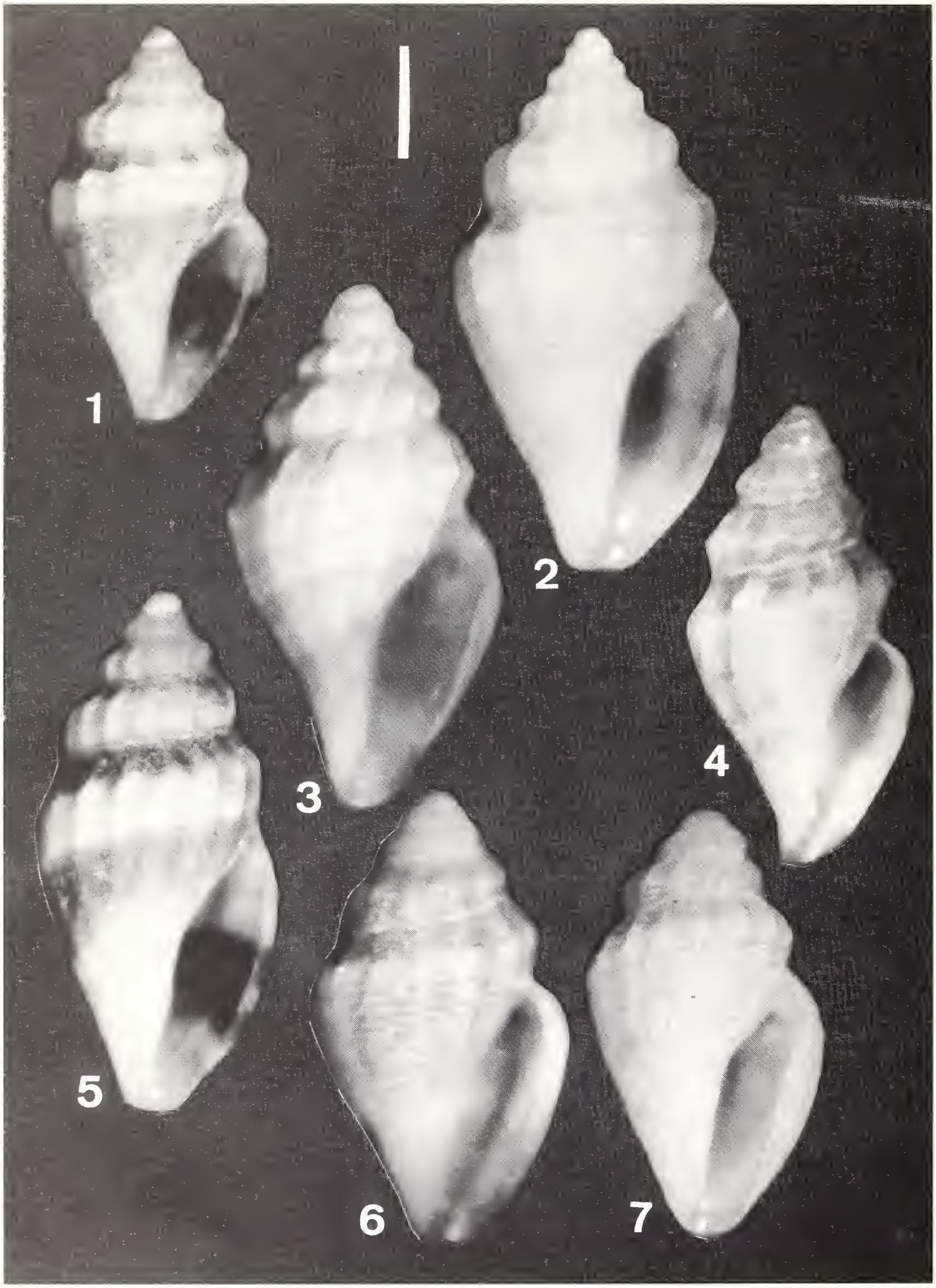
RESULTADOS

Género *Brachycythara* Woodring, 1928

Especie tipo por original designación: *Cythara gibba* Guppy, 1896.

Las características del género, según Powell (1966), son las siguientes: conchas pequeñas (4 - 9 mm), sólidas, bicónicas,turriculadas, con una angulación hacia la mitad de su longitud, con una abertura larga y estrecha, unidas gradualmente y con un canal anterior sencillo y sin separación. Protoconcha de 3 vueltas que se incrementan rápidamente, ápice pequeño, última vuelta con numerosos ribetes axiales. Labio externo algo fuerte, no varicoso.

Seno poco profundo a la altura del declive de la angulación. Callo parietal moderadamente fuerte, próximo al seno.



Figures 1-2. *Brachycythara biconica*. 1 - Patrón de color más habitual. 2 - Variedad de color claro. Figures 3-4. *B. barbarae*. Figure 5 - *B. alba*. Figures 6-7 - *B. multicinctata* spec. nov. (escala gráfica: 1 mm)

Hay especies en la fauna actual, y en el Plioceno y Mioceno de Centro América.

Brachycythara biconica (C. B. Adams, 1850)

(Figs. 1-2, 8-12)

Mangelia biconica C. B. Adams, 1850: 65.
Representada en Clench & Turner, 1950: lám. 32, fig. 2.

MATERIAL TIPO

Lectotipo, MCZ (177377).

OTRO MATERIAL ESTUDIADO

Cuba: 113 conchas, La Habana, en sedimentos de las playas (IDO); 79 conchas, Bahía de Cienfuegos, Cienfuegos y Rancho Luna (CFG); 1 concha, Puerto de Santa María (Camagüey) (IDO); 5 conchas, Rancho Luna, a 45 m (CER); 1 concha en Santa Cruz del Sur (CER); 2 conchas, Cuba (CER).

LOCALIDAD TIPO

Jamaica

DESCRIPCIÓN

Ver Adams (1850) y Clench & Turner (1950). Las conchas de Cuba, presentan las siguientes características morfológicas: la coloración (Fig. 1) es crema, con una banda algo más oscura en la zona subsutural en la que, frecuentemente, el color está más marcado en los espacios intermedios entre las costillas axiales; esta banda castaña llega hasta el ángulo de cada vuelta y, en la última vuelta, se puede apreciar otra banda más ancha en su mitad, apareciendo entre ambas una banda clara, frecuentemente con manchas blanco-leche y, a veces, con uno o dos cordoncillos castaños. También hay conchas con coloración mucho más clara (Fig. 2), aunque en ellas pueden apreciarse indicios de la coloración en bandas.

La protoconcha (Fig. 10) tiene un poco más de 2 vueltas de espira; la última tiene costillitas axiales oblicuas que al principio son difícilmente visibles y al final muy evidentes; el núcleo mide entre 108 y 112 mm.

La teloconcha se inicia con la aparición de la escultura espiral y una mayor separación de las costillas axiales. Su escultura está formada por gruesas costillas axiales con una angulación periférica mal definida; hay numerosos cordones espirales finos y algo elevados (Figs. 8-9) que, en la última vuelta, son unos 25 por debajo de la angulación; entre cada dos de estos cordoncillos principales, hay otros tres más finos y cruzados por estrías axiales que le dan un aspecto reticulado. La microescultura observable con gran aumento (Figs. 11-12) muestra los cordoncillos nodulosos, cordones más finos en los espacios entre ellos, la alineación vertical de los nódulos y la existencia, tanto en los cordoncillos como en los espacios intermedios, de una fina granulación microscópica. Por encima de la angulación periférica, los cordoncillos espirales son mucho más finos.

HÁBITAT Y DISTRIBUCIÓN

Recogida en sedimentos de fondos arenosos. Citada desde Carolina del Norte a Las Antillas (Cuba, Jamaica y Puerto Rico), el Golfo de México y la Península del Yucatán, hasta la costa norte de Sudamérica (Colombia y Aruba) por Adams (1850), Arango y Molina (1878-80), Dall & Simpson (1901), Warmke & Abbott (1961), Abbott (1974), Vokes & Vokes (1983), De Jong & Coomans (1988) y Díaz-Merlano & Puyana-Hegedus (1994), entre otros autores.

DISCUSIÓN

El holotipo es una concha de color crema amarillento en la que se pueden observar todavía las bandas de color que se mencionan en la descripción original. Tiene protoconcha bien conservada y es exacta en su morfología al material estudiado.

En el material de Cuba, sobre el modelo mencionado en la descripción, parece haber dos variedades de color que se encuentran tanto en la costa norte como en la sur, pero con un predominio diferente. En una de estas formas (Figs. 2 y 9), que suele ser de concha algo más grande, hay una atenuación de la coloración mencionada en la descripción, lo que hace que conchas no muy frescas aparezcan casi de color blanco. Esta forma es más abundante en el material de la Habana y, contrariamente a lo que se podría pensar, no representa el taxon *B. biconica alba* (C. B. Adams, 1850), ya que el lectotipo de esta especie tiene una protoconcha diferente. En la otra forma (Figs. 1 y 8), el color de las bandas es más oscuro y esto da a la concha un aspecto más bién crema o amarillento; las conchas de esta forma son algo más pequeñas y predominan en el material procedente del Sur de Cuba.

La comparación de la microescultura de ambas formas es muy similar (Figs. 11-12), aunque parece algo más acusada la granulación en la forma pequeña y más oscura; las protoconchas parecen también muy similares, aunque con una ligerísima diferencia del nucleo en favor de la forma clara y más grande. No habiendo otras diferencias importantes, las consideramos por el momento como pertenecientes al mismo taxon. Más completos estudios sobre material viviente de ambas podrá confirmar una relación conespecífica o no, y si son formas condicionadas por factores ecológicos, estacionales, etc. La presencia de ambas formas en Jamaica y en el norte y sur de Cuba parece descartar la posibilidad de considerarlas subespecies por aislamiento geográfico.

Brachycythara alba (C. B. Adams, 1850)

(Figs. 5, 13-15)

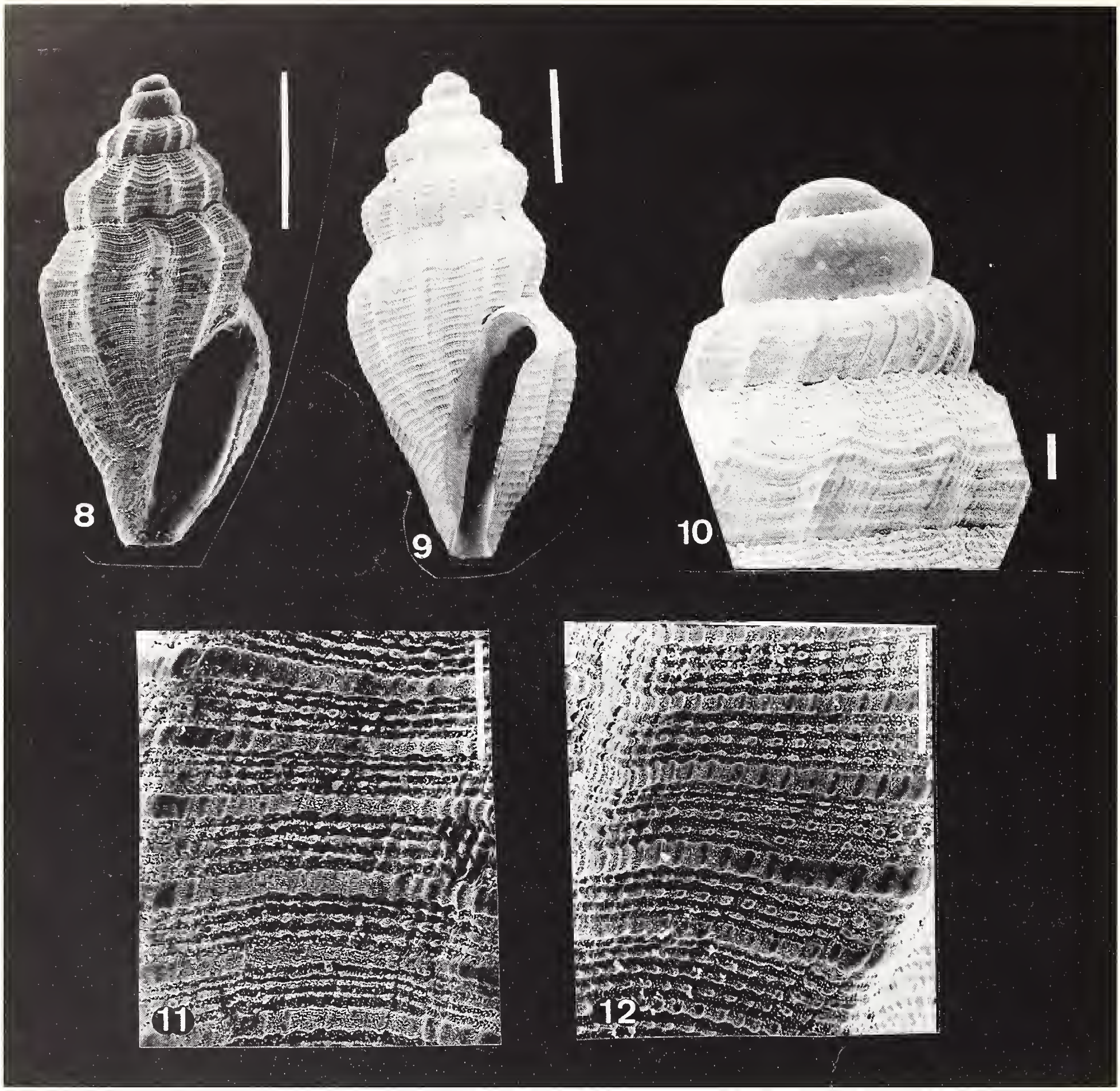
Magelia biconica var. *alba* C. B. Adams, 1850: 65.
Representada en Clench & Turner, 1950: lám. 32, fig. 1.

MATERIAL TIPO

Lectotipo, MCZ (186008).

OTRO MATERIAL ESTUDIADO

Cuba: 1 concha, Cabezo del Este, Camagüey (IDO); 4 conchas, Caibarien (IDO); 3 conchas, Cienfuegos (CFG).
República Dominicana: 7 conchas, 5 m (CER).



Figs 8-12. *B. biconica.* Fig. 8 . Concha con el patrón de color habitual con bandas. Fig. 9 Variedad de color claro. Fig. 10 - Protoconcha. Figs 11-12 - Microescultura. Fig. 11 - Microescultura de una concha de coloración típica. Fig. 13 - Microescultura de una concha de la variedad de color claro (escala gráfica: conchas: 1 mm; protoconcha: 0,1 µm; microescultura: 0,1 µm)

LOCALIDAD TIPO

Jamaica.

DESCRIPCIÓN

Concha (Figs. 5 y 13) pequeña, sólida, bicónica. La coloración es casi blanca en el lectotipo, pero en el material de Cuba, las conchas presentan una banda castaña en la zona subsutural, que puede ser uniforme o predominar en los espacios entre las costillas; en la mitad de la última vuelta aparece una nueva banda espiral de color. En la zona blanca que queda por debajo de la banda subsutural, suele haber un cordoncillo espiral de color castaño.

La protoconcha (Fig. 14) tiene un poco más de una vuelta de espira, que se hace muy ancha a partir del núcleo; es aparentemente lisa, pero con grandes aumentos se puede apreciar la existencia de gránulos pequeños y aislados, que se incrementan al

final de la misma donde, además, aparecen ondulaciones axiales; el núcleo mide 151 mm. Al comienzo de la protoconcha, suele aparecer una zona con coloración blanco-leche.

La teloconcha tiene unas 4 vueltas de espira. Su escultura está formada por gruesas costillas axiales, que presentan una angulación periférica algo marcada; la escultura espiral (Fig. 15) está formada por unos cordones principales espirales y finos, algo elevados y separados, dejando entre ellos, de tres a cinco cordoncillos más finos que están cruzados por estrías axiales que le dan aspecto reticulado. Las estrías axiales cruzan por encima de los cordones espirales más gruesos dándole aspecto aserrado o nodular. Los cordones principales son unos 17-19 por debajo de la angulación de la última vuelta; a veces, hay otro cordón algo más grande entre cada dos principales. Por encima de la angulación los cordones son más pequeños y están más juntos.

HÁBITAT Y DISTRIBUCIÓN

No hay datos sobre su hábitat. El material es escaso, pero de la existencia de una protoconcha muy corta parece deducirse un desarrollo larvario lecitotrófico y, probablemente, un área de dispersión pequeña.

DISCUSIÓN

B. alba ha sido considerada siempre una forma de color claro de *B. biconica*. Sin embargo el lectotipo está bien conservado y presenta una protoconcha más ancha en la primera vuelta que la de *B. biconica* y con una única vuelta de espira, por lo que se trata de una especie diferente. El material recolectado en Cuba es ligeramente más pequeño y con bandas de color muy marcadas, al contrario que el material de República Dominicana, que es totalmente blanco. Por todo ello, admitimos una variabilidad intraespecífica y pensamos que estas diferencias pueden ser de origen ecológico; escultura y protoconcha son iguales, por lo que las consideramos todas conespecíficas.

Brachycythara barbarae Lyons, 1972
(Figs. 3-4, 16-18)

Brachycythara barbarae LYONS, 1972: 4, figs. 3-4.

LOCALIDAD TIPO

Egmont Key, Florida.

MATERIAL TIPO

No examinado.

OTRO MATERIAL ESTUDIADO

Cuba: 10 conchas, Cienfuegos (CFG).

DESCRIPCIÓN

Ver LYONS (1972). La concha (Figs. 3-4 y 16) tiene un aspecto general similar a la de la especie anterior. A la descripción original añadimos la siguiente información: la protoconcha (Fig. 17) tiene 2 1/2 vueltas; la última, tiene costillitas axiales que son cruzadas en la parte inferior por cordoncillos espirales de tamaño similar; el núcleo mide 82 mm.

La teloconcha tiene una escultura formada por costillas axiales algo afiladas y con un ángulo bien evidente; no hay escultura espiral excepto un casi-cordón que une las costillas axiales a la altura de la angulación periférica. Estrías de crecimiento muy finas entre las costillas axiales, careciendo de cualquier otro tipo de microescultura (Fig. 18).

La coloración es blanquecina, con una banda espiral de color castaño claro en posición subsutural y cinco o seis, más estrechas, por debajo de la periferia. Hacia la base, una banda es bastante más ancha que las otras.

HÁBITAT Y DISTRIBUCIÓN

El material de Cienfuegos fué recolectado en sedimentos entre 20 y 30 metros de profundidad.

La localidad tipo es Florida y, probablemente, también es la especie que presentan DE JONG & COOMANS (1988) como *Brachycythara* sp.; por estos datos y su protoconcha con más de dos vueltas de espira, es presumible un área de distribución relativamente amplia dentro del Caribe.

DISCUSIÓN

La diferencia en el número de vueltas de la protoconcha en la descripción original y en nuestra descripción se debe sin duda al método empleado en la medición de la misma, y que nosotros hacemos a partir del núcleo (VERDUIN, 1977).

La carencia de microescultura (Fig. 18) diferencia *B. barbarae* de las restantes especies del complejo *B. biconica*; también por la presencia de un casi-cordón espiral en la angulación periférica, y en la aparición de cordoncillos espirales en la última vuelta de la protoconcha.

Brachycythara multicinctata sp. nov.
(Figs. 6-7, 19-21)

MATERIAL TIPO

Holotipo (Fig. 19) en el MNCN (nº 15.05/31935), recolectado entre 15 y 50 m, Cienfuegos; paratipos de la misma localidad en las siguientes colecciones: IDO (2), MCZ (2), CER (2) CFG (15).

OTRO MATERIAL ESTUDIADO

Cuba: 1 concha en la Habana (CER).

LOCALIDAD TIPO

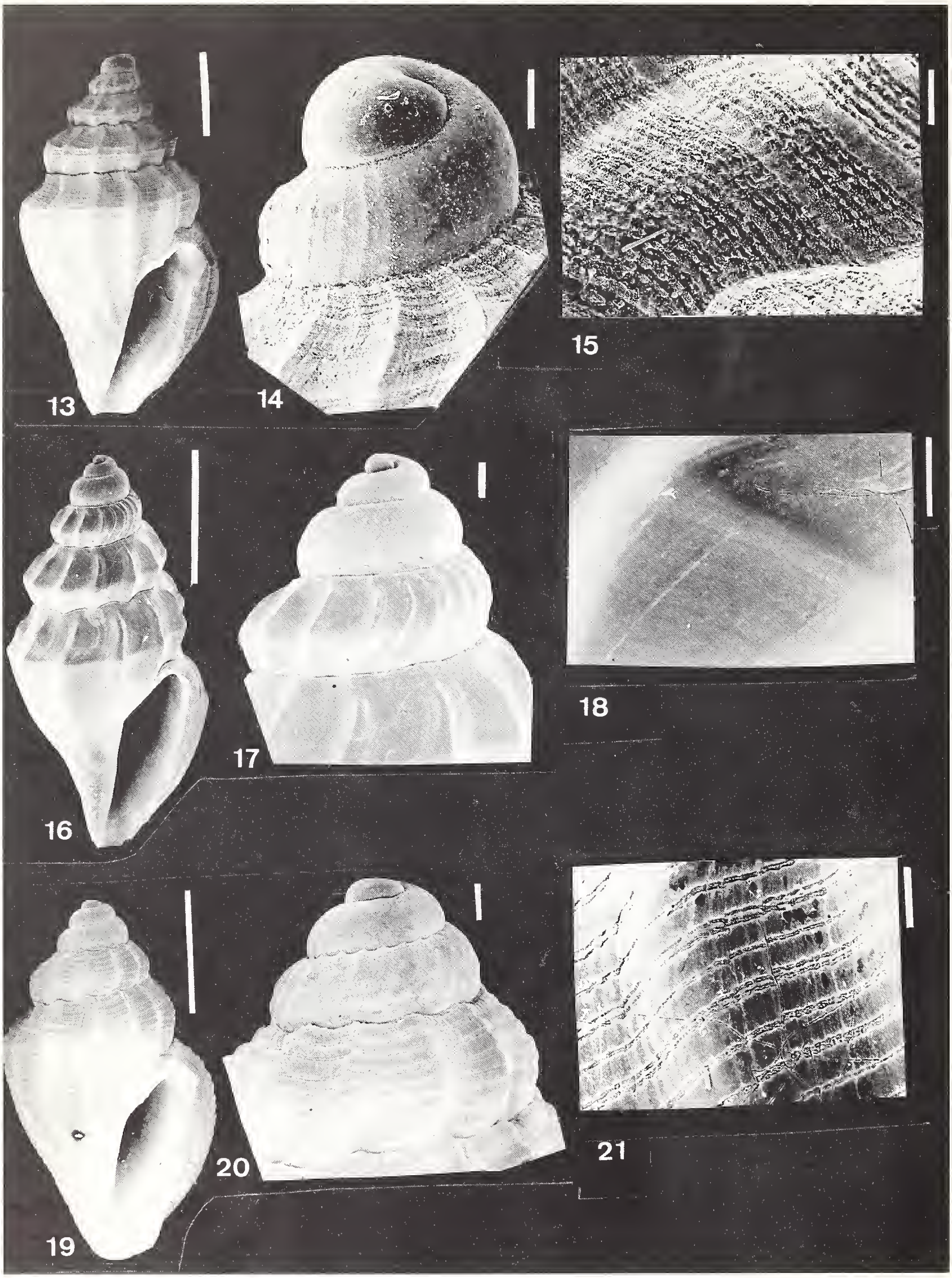
Cienfuegos, Cuba.

ETIMOLOGÍA

Hace referencia a la microescultura que asemeja la presencia de muchas cintas próximas entre sí.

DESCRIPCIÓN

La concha (Figs. 6-7 y 19) es bicónica, pequeña y sólida. Su coloración es crema, casi blanca, con una banda algo más oscura en la zona subsutural, que se aprecia mejor en la última vuelta.



Figs 13-15. *B. alba.* Fig. 13 - Holotipo. Fig. 14 - Protoconcha. Fig. 15 - Microescultura (escala gráfica: conchas: 1 mm; protoconcha: 0,1 mm; microescultura: 0,1 mm) Figs 16-18. *B. barbarae.* Fig. 16 - Concha. Fig. 17 - Protoconcha. Fig. 18 - Microescultura (escala gráfica: conchas: 1 mm; protoconcha: 0,1 mm; microescultura: 0,1 mm) Figs 19-21. *B. multicinctata* sp. nov. Fig. 19 - Holotipo. Fig. 20 - Protoconcha. Fig. 21 - Microescultura (escala gráfica: conchas: 1 mm; protoconcha: 0,1 mm; microescultura: 0,1 mm)

Las vueltas anteriores, tienen toda su extensión de color acastañado, teniendo la última de ellas una coloración siempre más clara en su parte inferior, lo que da a la concha una apariencia bicolor: oscura en su porción superior y clara por debajo.

La protoconcha (Fig. 20) tiene 2 vueltas y 1/2; la última de ellas tiene costillitas axiales; el núcleo mide 96 mm.

La teloconcha tiene una escultura formada por gruesas costillas axiales con angulación poco marcada; cordones espirales finos (Fig. 21), aplanados y muy juntos dejando, en el escaso espacio existente entre ellos, apenas uno o dos cordoncillos; todos ellos están cruzados en sentido axial por estrías muy débiles que le dan, con gran aumento, un aspecto ondulante. El número de cordones espirales es de unos 33 en la última vuelta (alrededor de 25 por debajo de la angulación) siendo por arriba y por debajo de la misma de un tamaño similar.

Abertura alargada; borde externo afilado con un engrosamiento labial un poco antes del final de la espira. Seno anal bien marcado pero no profundo. Canal sifonal corto y ancho.

HÁBITAT Y DISTRIBUCIÓN

Encontrada en sedimentos arenosos. Por su presencia en el norte y sur de Cuba y su protoconcha con más de dos vueltas de espira, es presumible su presencia en otras zonas del Caribe, aunque puede haber sido confundida hasta ahora con otras especies del grupo.

DISCUSIÓN

B. multicinctata spec. nov. se diferencia de *B. biconica* en que es más pequeña y tiene una microescultura diferente, con cordones espirales más gruesos que los espacios intermedios; la coloración es también algo diferente, castaña clara en la parte superior de la concha y blanca en la inferior, en vez de las bandas mencionadas en *B. biconica*; la protoconcha tiene el tamaño de su núcleo ligeramente menor. Se diferencia de *B. alba* por la microescultura que, en esta especie, está formada por cordoncillos finos; además *B. alba* tiene una protoconcha más gruesa y con sólo una vuelta de espira. *B. barbarae* es diferente por su coloración de bandas finas y porque carece de microescultura espiral.

AGRADECIMIENTOS

Al Museum of Comparative Zoology, Cambridge, por el envio del material tipo solicitado. A Raúl Fernández Garcés, por la aportación de la mayor parte del material estudiado. A Angel Guerra de Investigaciones Mariñas de Vigo, por darnos la posibilidad de la realización de las fotografías en el microscopio óptico; a Jesús Ortea y a Algel Valdés del Departamento de Organismos y Sistemas de la Universidad de Oviedo y a Bernardo Fernández Souto de Servicios Generales de Apoyo a la Investigación de la Universidad de A Coruña por las fotografías realizadas al MEB.

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Lavoro accettato il 2 Ottobre 1998

Paolo Quadri

12.1.1941 - 14.10.1998



Paolo Quadri ci ha lasciati. La sua presenza riempiva i luoghi da lui frequentati: era un punto di aggregazione per la sezione SIM di Milano, per la SIM intera, e per noi che lo frequentavamo.
Un male strano e refrattario ad ogni cura lo ha portato via in soli due mesi, proprio quando, essendo in pensione, poteva dedicarsi a tempo pieno alla malacologia e al riammodernamento della casa.
La passione per la malacologia, l'esuberanza e una grande voglia di fare, gli hanno permesso di mettere insieme in pochi anni una imponente collezione di conchiglie esotiche, mediterranee, e fossili italiani provenienti dal Pliocene della Liguria, Toscana, Piemonte, Emilia Romagna, Calabria e Sicilia: un vero patrimonio con esemplari di rara bellezza e tante microconchiglie.
Il materiale mediterraneo lo ha raccolto durante i soggiorni estivi in Campania, Sicilia, Isola del Giglio, Isola di Lampedusa, Tunisia, Cipro, Spagna. Ogni volta raccoglieva decine di chili di detrito, che esaminava durante la stagione invernale.
Il materiale di Cipro ha offerto lo spunto per tre lavori, preparati insieme all'amico Alberto Cecalupo, col quale aveva effettuato le ricerche. Il materiale di Lampedusa ha offerto lo spunto per un altro lavoro, presentato all'ultimo Congresso SIM di Firenze.
Nelle ricerche in mare, come in quelle sui depositi fossiliferi, era instancabile, quasi volesse sfruttare al massimo quei momenti. Mi redarguiva quando mi riposavo, tralasciando l'attività di ricerca.
Paolo era un ottimo conoscitore di microconchiglie, approfondiva sempre la sua ricerca tassonomica, consultando la vasta bibliografia di cui poteva disporre e scambiando idee e materiale con altri malacologi. Metteva volentieri la sua bibliografia a disposizione degli altri, ne faceva copie in più per gli amici a cui riteneva potesse interessare l'argomento.
Vista la grossa mole di materiale raccolto, molti esemplari, sia attuali che fossili, sono ancora in attesa di determinazione.
Paolo Quadri divenne socio della SIM nel 1985. Da sempre si è impegnato come organizzatore delle "Manifestazioni Natalizie" milanesi, a cui dedicava mesi di lavoro, stilando "Cataloghi" impreziositi da ottimi disegni, personalmente eseguiti per l'occasione. Il martedì sera non mancava alla riunione dei collezionisti milanesi, per discutere, determinare conchiglie, sognare viaggi malacologici. La sua prossima meta erano le Isole Maldive, a gennaio 1999.
Eletto nel Consiglio Direttivo della SIM nel 1997, ha ricoperto la carica di Tesoriere. A questa funzione si è dedicato con la meticolosità e la precisione tipici del suo carattere, in un delicato momento per la Società.
A ricordarlo nei testi di malacologia c'è una *Retusa quadrii* Cecalupo & Priora, 1992, ma ci auguriamo che la sua ricca collezione sia studiata da altri malacologi, e porti alla scoperta di altre nuove specie, perché il nome di Quadri continui a vivere, magari associato a una Alvania o un Raphitoma.
Alla famiglia Quadri le nostre più sentite condoglianze.

P. Micali

Pubblicazioni malacologiche di Paolo Quadri

1993 - Con E. Pracchia - Prima segnalazione di *Nassarius granum* (Lamarck, 1822) nel Pliocene italiano. *Bollettino malacologico*, Milano, 29 (1-4): 61-64.

1994 - Con A. Cecalupo - Contributo alla conoscenza malacologica per il nord dell'isola di Cipro. Parte I. *Bollettino malacologico*, Milano, 30 (1-4): 5-16.

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Bollettino Malacologico XXXIV [1998] Sommario - *Contents*

Allegato n. 3 al *Bollettino Malacologico*, Roma, **36** (5-8): I-XII, 2000 - Società Italiana di Malacologia

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a cura di Francesco Pusateri

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Direttore Responsabile: Carlo Smriglio

Coordinamento produzione: EVOLVER srl ROMA
Pre-stampa: FPM scrl ROMA
Stampa: ARTI GRAFICHE LA MODERNA ROMA

Finito di stampare il 22 Marzo 1999

ISSN 5678 8976